PACIFIC MARTEN (*Martes caurina*) AS AN APEX PREDATOR: THE HABITAT AND DIET ECOLOGY OF AN INSULAR POPULATION OF MESOCARNIVORE ON HAIDA GWAII

by

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Abstract

Pacific marten (*Martes caurina*) may benefit from invasive or non-native species that occur across some coastal areas of the Pacific Northwest. I used remote-camera trapping and stable-isotopes of carbon and nitrogen to infer resource-use strategies of marten on Haida Gwaii, British Columbia, Canada. Marten are more likely to be detected in 3 ha patches with less logging and optimal amounts of road and forest edge habitat, and areas close to marine shorelines and streams. Findings from bulk carbon and nitrogen stable-isotope analysis suggest that terrestrial fauna, including birds, deer, small mammals, and invertebrates, contribute the most to diet; marine invertebrates are the second-most important prey group. Marten consume salmon and berries seasonally, but these are a relatively minor component of the diet. Knowledge of habitat and diet ecology of this generalist, apex predator should be integrated into ecosystem-based management and conservation of the globally rare old-growth forests that remain relatively intact on Haida Gwaii.

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Chapter 1: Introduction

Background

Island ecosystems are often hot spots for biodiversity and endemism, and commonly lack large carnivores (Myers 1988; Frankham 1998; Roemer et al. 2009). Large carnivores regulate communities and maintain ecological function and biodiversity directly through predation, and indirectly through resource competition and trophic cascades (Estes 1998; Ritchie & Johnson 2009; Stier et al. 2016). In the absence of large carnivores, mesocarnivores can play the role of apex predator in relatively simple island ecosystems (Crooks & Soulé 1999; Prugh et al. 2009). The ecology of mesocarnivores as apex predators is not well-understood, yet has implications for the conservation of island biodiversity and should be considered in recovery strategies for endemic species at risk (Olson 1989).

Mesocarnivores are found in the order *Carnivora* and include small to mid-size (<15 kg) mammals, such as felids, canids, and mustelids (Roemer et al. 2009). Mesocarnivores display relatively high trophic plasticity and can perform a variety of ecosystem functions depending on exogenous forces, such as climate, plant species composition, competition and predation, and prey availability (Jordaan et al. 2019; Manlick et al. 2019). The energetic requirements of small-bodied predators are low, and can be met by omnivorous diets composed of plants, invertebrates, and small vertebrates (Carbone et al. 1999). Trophic plasticity and generalist foraging behaviour allow mesocarnivores to occupy diverse habitats with complex interspecific interactions at multiple trophic levels (Crait & Ben-David 2007; Shardlow 2014; Flaherty & Lawton 2019).

Marten (*Martes*) are one of the most ubiquitous *Mustelidae* genera and are found in most forests around the world (Aubry et al. 2012; Hisano et al. 2019; Twining et al. 2019). Two species of marten occupy forests of North America: Pacific marten (*Martes caurina*) and

American marten (*Martes Americana*; Dawson & Cook 2012; Manlick et al. 2019). Pacific marten are distributed west of the Rocky Mountains along coasts of the Pacific Northwest, from northern California to Alaska, and American marten are distributed from Alaska, east to the Atlantic coast, as far south as Idaho and Montana (Dawson et al. 2017). Hybridization occurs between the two groups in southern Montana and on Kuiu Island in Alaska (Small et al. 2003). A high degree of morphological and genetic differentiation among coastal island populations of Pacific marten, coupled with low within-population heterozygosity, reflect extended periods of isolation and divergence following sea level rise approximately 10,000 years ago (Small et al. 2003; Dawson et al. 2017).

Pacific marten differ from their allopatric sister species in several morphological characteristics (Dawson & Cook 2012). They have a wider zygomatic arch and are larger in body size (Giannico & Nagorsen 1989; Dawson & Cook 2012). Greater sexual dimorphism in skull size and body mass may reflect character displacement and greater niche breadth across island ecosystems that are absent of most other mesocarnivores that are sympatric with American marten (Giannico & Nagorsen 1989; Davies et al. 2007; Aubry et al. 2012).

Marten in North America are sensitive to forest fragmentation, and are found across landscapes containing greater amounts of contiguous forests with high structural complexity, including mature or old-growth coniferous forests (Thompson et al. 2012). Among coastal populations in the Pacific Northwest, this likely reflects adaptation to temperate rainforests with long return intervals between stand-replacing wildfires (Gaston et al. 2002; Lertzman et al. 2002; Delheimer et al. 2019). Marten in North America select home-ranges that contain larger patches of structurally complex forests and avoid areas with recent openings and early successional stand types (Slauson et al. 2007; Moriarty et al. 2016b). Marten spend more time foraging in complex

stands with dense, understory shrub cover where they perceive lower predation risk than in openings and stands with relatively little canopy cover (Slauson et al. 2007; Eriksson et al. 2019). Habitat structures normally associated with old forests, including stumps, snags, and large pieces of downed wood, provide foraging opportunities and are used for winter denning in areas with deep snow (Zielinski et al. 1983; Baker 1992; Delheimer et al. 2019).

Globally, old forests and their associated faunal communities are in decline (Lindenmayer et al. 2012b; Jones et al. 2018). Loss of large-diameter trees has greatly altered the structure and composition of temperate rainforests in the Pacific Northwest (Jones et al. 2018). On Haida Gwaii, a remote archipelago approximately 80 km offshore from northern British Columbia (BC), ~1700 km^2 of old-growth temperate rainforest has been logged in the last century, leaving ~5400 km^2 intact (Schoonmaker 1997; Gaston et al. 2002). Industrial logging has resulted in a reversal of age structure, from old forests with leading-tree species >250 years old, to young forests <50 years old (Gaston et al. 2002). A patchwork of clearcuts and extensive road networks have increased the density of forest edges, and altered habitat connectivity for species adapted to old-growth forests (Gaston et al. 2002; Waterhouse et al. 2017).

Relative to other islands in BC, the archipelago of Haida Gwaii contains a unique assemblage of mammal species, including 10 extant native species, and 10 introduced species (Golumbia 2000; Manlick et al. 2019). The native carnivore community consists of three species: river otter (*Lontra canadensis*), marten, and ermine (*Mustela erminea haidarum*; Foster 1963). An endemic subspecies of black bear (*Ursus americanus carlottae*) is native to the islands but is considered omnivorous (MacHutchon et al. 1998). With the exception of bats, the native small-mammal community consists only of Keen's mouse (*Peromyscus keeni*), of which there are two subspecies, and dusky shrew (*Sorex monticolus*), of which there are also two subspecies

(Golumbia 2000). In the absence of large carnivores that might regulate population dynamics of introduced herbivores, all forests on Haida Gwaii have been altered in structure and function by overbrowsing.

Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) were introduced to Haida Gwaii several times between the late-1800s and mid-1920s to provide local hunting opportunities (Pojar et al. 1980). Populations of deer irrupted in an environment containing no predators, abundant forage, and little competition (Pojar et al. 1980; Forsyth & Caley 2006; White et al. 2007). The only ungulate species native to Haida Gwaii was the now extinct (circa 1920-1930) Dawson's caribou (*Rangifer tarandus dawsoni*; Golumbia 2000). Deer show preference for tree seedlings, especially western redcedar (*Thuja plicata*), and prevent recruitment of seedlings into the canopy (Pojar et al. 1980). Unlogged forests on Haida Gwaii are now considered novel ecosystems because they exhibit old-growth characteristics in the canopy, yet contain understories and patterns of regeneration of leading-tree species that are radically altered by deer (Coates et al. 1985; Chollet et al. 2013b).

Overbrowsing has reduced the cover of understory herbaceous plants and replaced them with bryophytes and graminoids (Chollet et al. 2013a). The shift in species composition of primary producers has had indirect effects on abundance and diversity at higher trophic levels, a type of trophic cascade due, in part, to the absence of large carnivores (Polis et al. 2000; Martin et al. 2010). For example, overbrowsing, and subsequent loss of cover and forage, have reduced the abundance and diversity of invertebrates and songbirds associated with understory shrubs and flowering plants (Allombert et al. 2005a,b). The loss of understory plants may be connected with declines in populations of Sooty Grouse (*Dendragapus fuliginosus*), the only native species of gallinaceous bird on Haida Gwaii, and a primary prey of the coastal subspecies of Northern

Goshawk (*Accipiter gentilis laingi*; Doyle 2004; COSEWIC 2013; Parks Canada 2018). Clear-cut logging has reduced the amount and quality of nesting and foraging habitat for Northern Goshawk on Haida Gwaii, and multitrophic interactions resulting from overbrowsing by introduced deer have reduced the abundance and diversity of prey species relative to intact old-growth forests (Polis et al. 2000; Gaston et al. 2002; Allombert et al. 2005a). Northern Goshawk is listed as "Threatened" under the Species At Risk Act (SARA).

Contrastingly, high densities of introduced deer may be contributing to an increased abundance of marten, a native carnivore (Reid et al. 2000). Deer, likely scavenged primarily from natural winter-kills and roadside hunter-kills, are among the most frequently occurring prey species for marten sampled during winter on Haida Gwaii (Nagorsen et al. 1991). A relatively high density of Pacific marten supported by introduced deer, may limit recovery of species at risk, through intraguild competition and possibly intraguild predation (Polis & Holt 1989; Edie 2001). For example, marten share common prey with endemic Haida ermine (Nagorsen 2008), and may prey directly on the smaller, less abundant mustelid (Reid et al. 2000; although see Nagorsen 2006). Understanding the resource use strategies of marten as an apex predator in this uniquely altered island ecosystem will lead to more effective recovery strategies for species at risk, including Northern Goshawk and Haida ermine (Reid et al. 2000; Doyle 2004), and improved management of introduced species (McNicol 2019).

Research objectives

My thesis focuses on the habitat and diet ecology of Pacific marten on Haida Gwaii. The overall research objectives are to use camera traps to relate patterns of marten detections with habitat attributes and use stable-isotope analysis to quantify variability of marten diet. My specific objectives are to: 1) determine the relative importance of forest structure, human

disturbance, and access to marine resources for the distribution of marten across an area of Graham Island, Haida Gwaii, managed intensively for timber harvest; 2) estimate relative contributions of different food sources to marten diet across seasons and during overall lifetime; and 3) determine how diet varies with distance to marine resources, including salmon-bearing streams and marine shorelines.

Thesis structure

My thesis is organized into four separate chapters. In Chapter 1, "Introduction", I present an overview of the ecology of marten in North America, as well as relevant background information on the habitat and diet ecology of Pacific marten in northwestern North America. I position marten as an apex predator in the unique ecological context of Haida Gwaii and outline the research objectives and thesis structure.

In Chapter 2, "Detections at remote-camera stations reveal habitat use strategies of Pacific marten on southeast Graham Island, Haida Gwaii", I examine patterns of habitat use in relation to forest structure, human disturbance, and access to marine resources at multiple spatial scales. I first develop conceptual models representing competing *a priori* hypotheses concerning habitat use within an intensively managed area of Graham Island, Haida Gwaii. I then use mixed-effects logistic regression and an information theoretic approach to determine relative support for each explanatory model hypothesis.

In Chapter 3, "Using stable-isotope analysis to investigate spatial and temporal variability in the diet of Pacific marten on Haida Gwaii", I use stable-isotopes of carbon and nitrogen to estimate the diet of marten on Haida Gwaii and to determine how diet changes seasonally and with different access to marine resources. I use Bayesian isotopic mixing models to estimate relative contributions of four diet items: salmon, marine invertebrates, terrestrial fauna (beetles,

mammals, and birds), and berries. First, I evaluate seasonal variability in diet by comparing estimated relative contributions of diet items among tissue types: distal guard hair, proximal guard hair, muscle, and bone. Second, I determine how diet varies with different levels of access to marine resources by comparing diet estimates among marten sampled in areas with relatively low, moderate, and high densities of salmon-bearing streams and at different distances to marine shorelines. Finally, I compare stable-isotope values and diet estimates between males and females, between young of the year and adults, and between different categories of nutritional condition.

In Chapter 4, "Research Summary", I provide a synthesis of the habitat use and diet results and position my findings in the broader context of mesocarnivore research. Further, I address the limitations of this study and make recommendations for future research. I conclude by discussing implications for management of forest values and conservation of species at risk on Haida Gwaii.

Chapter 2: Detections at remote-camera stations reveal habitat use strategies of Pacific marten on southeast Graham Island, Haida Gwaii

Introduction

Marten (*Martes* spp.) are considered specialists of mature forests, as well as an indicator of the health of forests in North America (Spencer et al. 1983; Zielinski et al. 2005; Moriarty et al. 2016b). Pacific marten (*M. caurina*) den in standing, large-diameter live and dead trees found in the temperate coastal rainforests of the Pacific Northwest (Delheimer et al. 2019). These forests rarely experience large-scale natural disturbance events such as wildfire and insect outbreaks, and the natural-disturbance regime consists mainly of gap dynamics resulting from individual tree mortality (Franklin et al. 1987; Lertzman et al. 2002). It takes hundreds of years to develop standing live and dead trees of suitable diameter to produce cavities for marten to use as dens, and within short periods of time (<10 years) these trees can transition from standing to downed wood (Lindenmayer et al. 2012a; Delheimer et al. 2019).

Throughout much of their range in North America, marten have experienced declines in distribution and abundance due to habitat loss resulting from timber harvesting (Schorger 1942; Zielinski et al. 2005; Lavoie et al. 2019). Forestry practices involving broad-scale removal of large-diameter trees reduces the amount of suitable habitat for marten and other specialists of old forests (Lavoie et al. 2019). The changes to the landscape caused by forest management are inconsistent with the natural disturbance regime that maintains the ecological structure and function associated with large-diameter trees (Lindenmayer et al. 2012a).

Haida Gwaii is a remote archipelago off the northern coast of British Columbia (BC) and contains a large proportion of the last remaining coastal temperate rainforests in the world (Gaston et al. 2002; Dawson et al. 2017). These forests function as habitat for many endemic

species that are genetically and morphologically distinct from their mainland counterparts (Byun & Reimchen 1997). Endemic species on the islands are vulnerable to extirpation and extinction due to low abundance and functional isolation (Frankham 1998; COSEWIC 2006; Waterhouse et al. 2017). Industrial logging coupled with overbrowsing by introduced Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) have permanently altered the distribution and quality of old-growth habitat, increasing the risk of population declines among island endemics adapted to old forests (Gaston et al. 2002; Allombert et al. 2005a; Chollet et al. 2013a).

In contrast, Pacific marten on Haida Gwaii may be increasing in abundance despite recent anthropogenic disturbance (Reid et al. 2000). Introduced deer are the most frequently occurring prey species for marten sampled during winter on Haida Gwaii (Nagorsen et al. 1991; Nagorsen 2006). Forestry activities that result in greater amounts of early seral forests, interspersed with patches of remnant old-growth stands, may increase the carrying capacity for deer (Côté et al. 2004). High densities of introduced deer and the resulting carrion could increase the reproductive output and survival of marten (Rose & Polis 1998; Carlson et al. 2014). Further, forests along marine shorelines may support higher population densities of marten relative to inland habitats due to increased access to marine-derived nutrients (Rose & Polis 1998). The ecology of marten, an apex predator in this context, may have consequences for endemic species that are at risk of extinction or extirpation (Reid et al. 2000). However, there have been few studies of the ecology of this insular population of mesocarnivore (Nagorsen et al. 1991; Manlick et al. 2019).

Marten on Haida Gwaii may demonstrate unique habitat use strategies that reflect adaptations to a maritime climate (Baker 1992; Yom-Tov et al. 2008; Baltensperger et al. 2017). A maritime climate results in mean annual temperatures between 7–8°C and no persistent winter snowpack at low elevations (Banner et al. 2014). Therefore, access to subnivean spaces for

resting and hunting might not limit the distribution of marten on Haida Gwaii as it does in mainland ecosystems with greater snowfall and lower winter temperatures (Thompson & Colgan 1994). For example, the stumps, snags, and large pieces of downed wood that marten use as winter denning structures in areas with deep snow may not be required at lower elevations in maritime ecosystems with little snowpack (Nagorsen et al. 1989; Baker 1992).

Pacific marten may not be as dependent on old-growth forests when prey are widely available and predation risk is low. On Vancouver Island, BC, Pacific marten use second-growth forests more frequently than observed elsewhere, and do not select for mature or old-growth forests (Baker 1992). Deer mice (*Peromyscus* spp.) are the most important mammalian prey for marten on Vancouver Island, and are most abundant in young seral stages (Nagorsen et al. 1989; Baker 1992). Marten may perceive less risk of predation in second-growth stands on Vancouver Island and Haida Gwaii, because of the absence of several predators of mainland marten, including bobcat and coyote (Thompson & Colgan 1994; Bull & Heater 2000; Moriarty et al. 2016b). The only natural predators of marten on Haida Gwaii are avian (Bull & Heater 2000); therefore, risk of predation may not limit marten to habitats with escape routes and cover from predators, as it does in regions with a greater diversity of large carnivores (Buskirk 1984; Moriarty et al. 2015).

I used an array of remote-cameras to systematically detect marten across inland and nearshore forest habitats located across the southern portion of Graham Island, Haida Gwaii, during the winters of 2017 and 2018. The research was designed to reveal the habitat use strategies of marten located in a region of the Haida Gwaii archipelago with extensive forest harvesting. I hypothesized that detections of marten at camera stations would increase with increased forest structural complexity and stand age, decrease with increased human disturbance

and forest edge, and increase with increased access to marine and riparian resources. I examined habitat use at two spatial scales relevant to marten ecology: choice of home-range location (second-order selection) and choice of patches within a home-range (third-order selection; Shirk et al. 2012).

Methods

Study Area

The study area was located across an 842-km^2 portion of southern Graham Island, Haida Gwaii (Figure 1). Forests in the study area below 350 m elevation were found within the Coastal Western Hemlock, Submontane Wet Hypermaritime (CWHwh1) Biogeoclimatic Ecosystem Classification (BEC) variant (Pojar et al. 1987). Above 350 m elevation, forests occurred within the Coastal Western Hemlock, Montane Wet Hypermaritime (CWHwh2) variant (Pojar et al. 1987; Banner et al. 2014). Sparse Mountain Hemlock Wet Hypermaritime (MHwh) occurred between 500-900 m elevation (Banner et al. 2014).

The study area was covered mostly in coniferous forests with a variety of non-forested ecosystems including intertidal mudflats and rocky marine shorelines, subalpine meadows, and wetlands, including bogs, fens, marshes, and swamps (Gaston et al. 2002; Banner et al. 2014). Coniferous forests were dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*) at low elevations, with mountain hemlock (*Tsuga mertensiana*) and yellow cedar (*Chamaecyparis nootkatensis*) increasingly abundant at higher elevations (Pojar & MacKinnon 1994; Banner et al. 2014). Western yew (*Taxus brevifolia*) was present in the subcanopy of some old coniferous forests (Banner et al. 2014). Red alder (*Alnus rubra*) was common in recently disturbed areas such as floodplains, landslides, and along roads (Pojar & MacKinnon 1994).

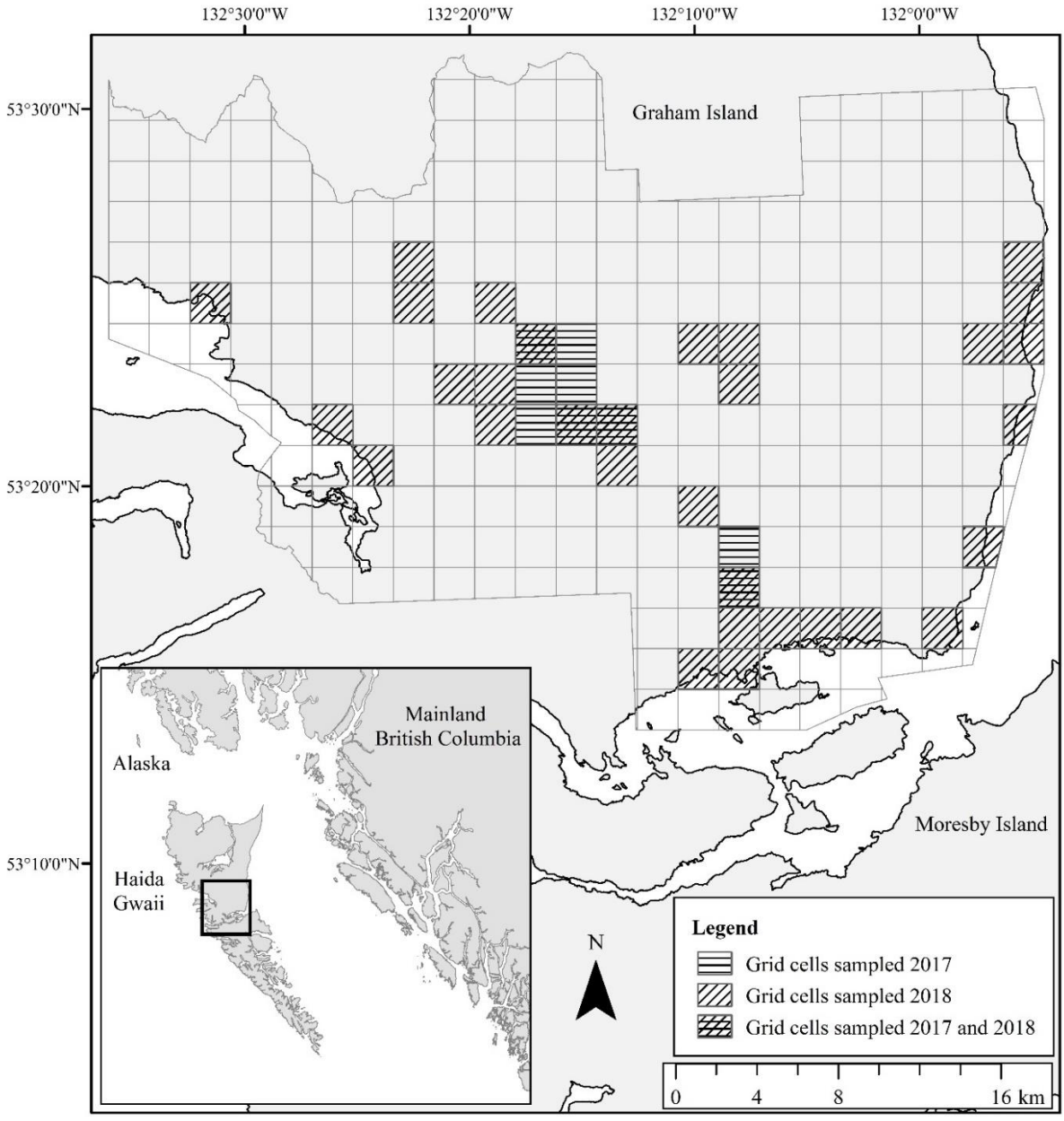


Figure 1. Study area (outlined in grey) with 4-km^2 grid cells used to distribute camera trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, in 2017 (horizontal crosshatch) and 2018 (diagonal crosshatch).

The mean annual temperature of the study area was ~8 ± 1.4 ˚C (Government of Canada Environment and Climate Change 2013). The east coast of Graham Island was dry relative to the west coast due to a rain shadow caused by the Queen Charlotte Ranges (Banner et al. 2014). Total annual rainfall was ~130 cm. Total annual snowfall at low elevations was ~38 cm, although at 300–600 m elevation monthly snowfall reached 10–20 cm with persisting snowpack (Banner et al. 2014).

The study area included two large protected areas co-managed by the Haida Nation and the Province of BC. Haida people continued traditional cultural use of protected areas, including monumental cedar harvesting, food and medicine gathering, fishing, and hunting. The Tlall Conservancy/Heritage Site in the northeast portion was 162 km^2 in area and contained the Tlell River watershed (Haida Nation & Province of British Columbia 2011a). Tlall contained unique wetlands and old-growth Sitka spruce floodplain forests. The Yaaguun Suu Conservancy/Heritage Site was located <10 km southwest of Tlall in the western portion of the study locale, and was 80 km^2 in area (Haida Nation & Province of British Columbia 2011b). Yaaguun Suu contained the headwaters of the Yakoun River watershed, as well as Yakoun Lake, which was surrounded by intact old-growth stands of Sitka spruce, redcedar, and hemlock, as well as large-diameter yew in the understory.

The study area included relatively high levels of recent anthropogenic disturbance. Industrial logging produced stand ages that were younger than would be present under the natural disturbance regime (Gaston et al. 2002; Lertzman et al. 2002; Lindenmayer & Laurance 2017). Managed stands on 60-year rotations and forestry roads fragmented remnant patches of old forests and provided abundant edge habitat for deer and introduced plant species (Gaston et al. 2002). Human settlements covered ~41 km^2 in land area with ~1700 residents (Government

of Canada Statistics Canada 2017), and a highway followed the shoreline along the east coast of Graham Island. Residents with chicken coops have killed marten as pests and marten have been regularly killed by vehicles on the highway. Though martens are commercially trapped on Graham Island, trapping did not take place within the study area during the sampling period.

Sampling

I used a systematic sampling design to investigate habitat use by marten during winter (Burton et al. 2015). I used a 4-km^2 grid derived from the National Topographic System (NTS) to distribute trap stations that contained remotely activated cameras and baited hair snares. The 4-km^2 grid cell is similar in size to estimates of Pacific marten home-ranges (Baker 1992; Moriarty et al. 2016b; Linnell et al. 2018). I split 4-km^2 grid cells into 1-km^2 cells to maximise the number of stations that I could monitor. I attempted to install cameras systematically in the center of each grid cell, though logistical constraints, including road access and elevation (<300 m), ultimately guided the placement of cameras. Camera stations were installed in areas with active timber harvesting, as well as in protected forests in Yaaguun Suu and bordering Tlall. Cameras were active from January 12–April 25, during 2017 and 2018. The probability of detecting marten was greatest during winter and black bears were much less active at this time (Nelson et al. 1983; Zielinski et al. 2015). During the 2017 and 2018 sampling periods, I used 26 stations distributed among nine, 4-km^2 grid cells, and 46 stations placed within 31, 4-km^2 grid cells, respectively. Over the course of the study, I sampled 72 different stations distributed across 36 grid cells; four 4-km^2 grid cells were sampled in both years.

Each station contained one camera cabled to a tree of at least 20-cm diameter (measured at 1.3 m height) and secured 0.5–1 m above the ground. I used Reconyx PC900 and HC600 Hyperfire Professional wildlife cameras with a ‘rapid-fire’ burst of five photos set to ‘motion-

trigger' with 'no delay', 'high' sensitivity, and a 3.1 mega pixel (MP) resolution (RECONYX, Inc., Holmen, WI). Each camera had two different hair snares in the field of view, with the exception of six stations deployed at the edges of forests adjacent to the supralittoral zones of marine shorelines, which were each aimed at a single hair snare. Hair snares passively collected marten hair for stable-isotope analysis of diet (Chapter 3). I used a long-distance olfactory lure to call marten to the station and I baited hair snares with commercial chicken wings to attract marten to the camera zone of detection (Mowat & Paetkau 2002; Schwartz et al. 2006; Stewart et al. 2019). The olfactory lure consisted of glycerine, commercial fisher and marten lure, ground beaver castor, anise oil, skunk essence, and fish oil. Previous research has demonstrated that positive response bias due to bait and lure is minimal compared to the benefits of increased detection probability (Stewart et al. 2019).

Field crews visited trap stations between two and five times during each sampling period. During each visit, crews refreshed lure and bait, and replaced the memory cards, batteries, and desiccant in the cameras, and recorded signs of station disturbance. This study was approved by the Animal Care and Use Committee, University of Northern British Columbia (Protocol Number: 2017-09) and under the authority of the British Columbia Ministry of Forests, Lands, Natural Resource Operations, and Rural Development.

Data Analysis

I downloaded photos and used MapView Professional (RECONYX, Inc., Holmen, WI) and MS Access (MS Office 2016) to store and classify individual photos. I reduced the photo data to a binary outcome (detection or non-detection) for each 2-week interval for each trap station (Tigner et al. 2015). Pacific marten can take up to 2 weeks to move throughout their

entire territory; therefore, 2-week sampling intervals likely reduced the number of false negatives (Moriarty et al. 2017).

I developed a set of *a priori* hypotheses to explain the patterns in habitat use by marten. I selected explanatory variables that represented different measures of marten habitat quality, as well as measures of sampling bias (Table 1). I constructed 14 conceptual models representing four categories of explanatory factors: sampling bias, forest structure, topography (distance to marine shorelines and riparian areas), and human disturbance (Table 2; Burnham et al. 2011; Tweedy et al. 2019). Marten select resources at multiple spatial scales to meet different life history requirements (Bissonette 1997; Porter et al. 2005; Thompson et al. 2012). Thus, I constructed conceptual models at two spatial scales: 100-m and 1000-m radius circles centered on each camera station (Zhao et al. 2012). I used the results from past studies of marten habitat relationships to select the spatial scale of each variable and model (Tables 1 and 2).

Sampling bias

I included three covariates in all models to control for potential image bias associated with the deployment and monitoring of cameras (Burton et al. 2015). For example, I replenished bait and re-applied lure more frequently in 2018 than in 2017. Therefore, I expected detection rates to increase between 2017 and 2018 (Sirén et al. 2016). I used a binary categorical variable to track the year of sampling (2017 or 2018) for each camera station. The density of camera stations was variable between years and among stations within each year of sampling. Multiple stations within a home-range increases the density of olfactory lure and provides more opportunities for marten to develop positive trap responses (Nichols et al. 1984; Burton et al. 2015; Stewart et al. 2019).

Table 1. Category, scale of measurement, and description for each explanatory variable (units in brackets) used in logistic regression models to predict Pacific marten detections at trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, during winters of 2017 and 2018.

Category	Variable	Scale	Description (units)
Sampling bias	Station clustering	Na	binary categorical variable representing grid cells with one or multiple camera stations
	Year of sampling	Na	binary categorical variable (2017 or 2018)
	Average temperature	Na	temperature during 2-week intervals (°C)
	Station density	1000-m	number of stations per 1-km^2 area
Forest structure	Average tree height*	100-m	predicted mean height of trees indicated from LiDAR first returns (m)
	Area >20 m height*	1000-m	predicted percent area with mean height of LiDAR first returns >20 m (%)
	Area 10–20 m height*	1000-m	predicted percent area with mean tree height between 10–20 m indicated from LiDAR (%)
	Percent cover 0–1 m height*	100-m & 1000-m	shrub cover indicated from mean percent of LiDAR first returns between 0–1 m height (%)
	Area >45% canopy cover	1000-m	percent area with leading tree species >45% canopy cover (%)
	Canopy cover*	100-m	percent canopy cover indicated from LiDAR first returns >1.37 m height (%)
	Average age	100-m	mean age of leading tree species (years)
	Area >250 years old	1000-m	area with age of leading tree species >250 (%)
Topography	Distance to marine shoreline ᑫ	100-m	mean distance of sampling unit from marine shoreline, represented as a two-term quadratic term (km)
	Distance to riparian area ᑫ	100-m	mean distance of sampling unit from riparian areas, represented as a two-term quadratic term (km)
Human disturbance	Area cut (linear)	100-m	area harvested within 30 years of sampling (%)
	Area cut ᑫ	1000-m	area harvested within 30 years of sampling represented as a two-term quadratic term (%)
	Forest edge density ᑫ	100-m & 1000-m	density of forest edge, represented as a two-term quadratic term (km/km^2)
	Road density ᑫ	100-m & 1000-m	mean line density of roads, represented as a two-term quadratic term (km/km^2)
	Active road density	100-m & 1000-m	mean line density of active roads (km/km^2)
	Abandoned road density ᑫ	100-m & 1000-m	mean line density of unused roads, represented as a two-term quadratic term (km/km^2)

* indicates predicted LiDAR metrics

ᑫ indicates two-term quadratic functions.

Table 2. Explanatory category, conceptual models (with references), and combinations of fixed effects (with scale of measurement) used in logistic regression models to predict detections of Pacific marten at trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, during the winters of 2017 and 2018.

Category	Model	Model Structure (scale)
Sampling bias	Sampling bias[1,2]	Station clustering + Year of sampling + Average temperature (aspatial)
	Camera station density[3]	Station density + Station clustering + Year of sampling + Average temperature (1000-m)
Forest structure	Tree height[4,5]	Area >20 m height*+ Area 10–20 m height* + Station clustering + Year of sampling + Average temperature (1000-m)
	Canopy cover[6,7]	Area >45% canopy cover + Station clustering + Year of sampling + Average temperature (1000-m)
	Age of leading tree species[8,9]	Average age + Station clustering + Year of sampling + Average temperature (100-m)
	Cover and tree height[4,8]	Canopy cover*+ Average tree height* + Percent cover 0–1 m height* + Station clustering + Year of sampling + Average temperature (100-m)
	Cover, tree height, and age[4,10]	Area >45% canopy cover + Area 10–20 m height* + Area >250 years old + Station clustering + Year of sampling + Average temperature (1000-m)
	Near-ground cover[3,11]	Percent cover 0–1 m height* + Station clustering + Year of sampling + Average temperature (1000-m)
Topography	Distance to marine shoreline[12,13]	Distance to marine shoreline ^{q} + Station clustering + Year of sampling + Average temperature (100-m)
	Distance to riparian area[6,14]	Distance to riparian area ^{q} + Station clustering + Year of sampling + Average temperature (100-m)
Human disturbance	Road density and area harvested[14,15]	Road density ^{q} + Area cut ^{q} + Station clustering + Year of sampling + Average temperature (1000-m)
	Active and abandoned roads, and forest edge[16,17]	Active road density + Abandoned road density ^{q} + Forest edge density ^{q} + Station clustering + Year of sampling + Average temperature (1000-m)
	Area harvested, forest edge, and road density[14,15,17]	Area cut + Forest edge density ^{q} + Road density ^{q} + Station clustering + Year of sampling + Average temperature (100-m)
	Active and abandoned roads[14]	Abandoned road density ^{q} + Active road density + Station clustering + Year of sampling + Average temperature (100-m)

* indicates predicted LiDAR metrics

^{q} indicates two-term quadratic functions.

Sources: 1. (Thompson & Colgan 1994) 2. (Sirén et al. 2016) 3. (Slauson et al. 2007) 4. (Spencer et al. 1983) 5. (Payer & Harrison 2003) 6. (Buskirk et al. 1989) 7. (Corn & Raphael 1992) 8. (Mowat 2006) 9. (Andruskiw et al. 2008) 10. (Moriarty et al. 2016b) 11. (Bull & Heater 2000) 12. (Foster 1963) 13. (Nagorsen et al. 1991) 14. (Shirk et al. 2012) 15. (Baker 1992) 16. (Hargis et al. 1999) 17. (Potvin et al. 2000)

I expected marten to be detected more frequently at camera stations located within 4-km^2 grid cells containing more than one station, as opposed to grid cells with only one station (Burton et al. 2015; Sirén et al. 2016). Similarly, I expected marten detections to be positively correlated with the density of camera stations. I used a binary categorical variable, 'Station clustering', to distinguish between camera grid cells with one or multiple camera stations (Table 1). Further, I calculated the mean density of stations around each station at the 1000-m scale for each year of sampling (Table 1).

Temperature and season may affect animal movement and behaviour (Zielinski et al. 1983, 2009, 2015). As temperature and daylight hours change, so do patterns in marten activity and potential detections at cameras (Thompson & Colgan 1994; Zielinski et al. 2015). Thus, I included a covariate representing the average temperature for each 2-week sampling interval, as recorded by the cameras (Table 1).

Forest structure

Marten select home-ranges with mostly old-growth or late-mature forests (Moriarty et al. 2016b). These forests contain complex woody structures that marten require to meet many life history requirements including foraging, denning, and escaping from predators (Spencer et al. 1983; Mowat 2006; Andruskiw et al. 2008). I hypothesized that marten would be detected more frequently in areas with older developmental stages, greater canopy cover, taller trees, and greater cover of understory shrubs (Buskirk et al. 1989; Corn & Raphael 1992; Aubry et al. 2012). Tree height is a proxy of forest age and structure. Thus, I calculated the percent area of trees >20 m in height within a radius of 1000 m of each camera trap (Table 1; Spencer et al. 1983; Payer & Harrison 2003; Banner et al. 2014).

Much of the study area is made up of second-growth, Sitka spruce forests (Gaston et al. 2002; Banner et al. 2014). These stands are even-aged and lack the large-diameter, tall trees of uncut old-growth stands. However, marten have been shown to select home-ranges in areas of high structural complexity, regardless of forest age or composition (Poole et al. 2004; Eriksson et al. 2019). Relatively young, second-growth forests may contain sufficient near-ground structural complexity and canopy cover to provide marten with access to prey, cover from predators, as well as resting and denning sites (Buskirk et al. 1989; Corn & Raphael 1992; Bull & Heater 2001). Furthermore, marten may perceive less risk of predation in second-growth stands on Haida Gwaii due to the absence of several predators of mainland marten, including bobcat and coyote (Thompson & Colgan 1994; Bull & Heater 2000; Moriarty et al. 2016b). I represented second-growth by calculating the percent area of the stand with average height of trees between 10–20 m around each station at the 1000-m scale (Table 1; Payer & Harrison 2003; Banner et al. 2014).

I used Light Detection and Ranging (LiDAR) and Vegetation Resource Inventory (VRI; Ministry of Forests, Lands, Natural Resource Operations and Rural Development) data to calculate metrics that represented the canopy and understory structure around each station. LiDAR is useful for modelling the vertical structure of forests and has proven effective at characterizing habitat for forest-dwelling mesocarnivores, including Pacific marten (Lim et al. 2003; Zhao et al. 2012; Tweedy et al. 2019). LiDAR surveys were flown between 2015–2016 using a RIEGL LMS-Q1560 sensor on a fixed-wing aircraft, with an average point density of eight pulses/m^2 (RIEGL Laser Measurement Systems, Horn, Austria). LiDAR metrics were derived using LAStools (rapidlasso GmbH, version 1.4).

Some trap stations were located outside of areas with LiDAR coverage; therefore, I used multiple linear regression to predict values of LiDAR metrics from VRI and topographic data (STATA, version 14, StataCorp.). I used LiDAR and corresponding VRI data from random locations across the study area at the 100-m scale (n = 200) and 1000-m scale (n = 100) to develop predictive linear equations for each LiDAR metric. I maximized the R^2 value for each linear equation while avoiding excessive multicollinearity. For comparisons between predicted and observed LiDAR values at camera stations (n = 21), I first tested for violations of assumptions of normality (Shapiro-Wilk test) and equal variances (F-test). Assumptions of normality were not met; therefore, I used a Wilcoxon signed-rank test to compare predicted and observed LiDAR values at camera stations. I conservatively included predicted metrics as covariates in habitat models if the distributions of predicted and observed values were not significantly different ($\alpha = 0.05$). I used the VRI data for forest age and structure when LiDAR values could not be accurately predicted (Table 1).

Topography

Marine intertidal zones are a source of nutrients that may subsidize the winter diets of generalist predators, including marten (Rose & Polis 1998; Roemer et al. 2009). I hypothesized that marten would be more likely to spend time foraging in patches of forest (100-m scale) close to marine shorelines, as evidenced by increased detections at stations adjacent to supralittoral zones (Foster 1963; Nagorsen et al. 1991). I expected this relationship to be nonlinear, and the effect of proximity to marine shoreline on probability of detection to decrease at stations located farther inland.

Riparian areas are important foraging habitat for marten in North America, due to high densities of preferred prey, including small mammals and birds (Spencer et al. 1983). Further, in

coastal areas of the Pacific Northwest, marten with home-ranges close to salmon streams rely on salmon carcasses as an important source of food when small mammal abundance is low (Ben-David et al. 1997). I hypothesized that marten would be more likely to forage in patches (100-m scale) near riparian areas due to increased prey density (Buskirk et al. 1989; Shirk et al. 2012). Similar to the effect of marine shorelines, I expected this relationship to be nonlinear and for the effect of proximity to riparian areas to decrease at greater distances. I measured the Euclidean distance from each station to the nearest riparian area (Stream Centreline Network, DataBC Distribution Service) and marine shoreline derived from a digital elevation model (DEM).

Human disturbance

Marten may select home-ranges containing some clearcutting as foraging habitat due to increased availability of some prey species, including deer mice (Baker 1992). There may also be sufficient near-ground structure in clearcuts to provide marten with denning opportunities (Slauson et al. 2007). I hypothesized that marten would demonstrate a non-linear, concave response to the proportion of clearcuts within their home-ranges (1000-m scale) and a linear response within patches (100-m scale; Table 1). Some access to cutblocks or early successional forests may provide hunting and denning habitat, but an over-abundance of cutblocks may reduce access to interior forest habitat and the associated habitat features such as standing dead trees and ground structure (Potvin et al. 2000). I calculated the percent of the area that had been harvested for timber within 30 years of sampling within 100-m and 1000-m distances from each station (Consolidated Cutblock Layer, DataBC Distribution Service).

I constructed models to represent competing hypotheses that represented the use of roads by marten (Table 2). Generally, marten avoid open areas and areas of high human disturbance (Hargis et al. 1999; Potvin et al. 2000). Therefore, I expected marten to select home-ranges with

low densities of maintained roads and avoid areas of high road density due to the pulse stressor of vehicle traffic (Mowat 2006; Slauson et al. 2017). However, roads provide access to hunter-killed deer carcasses, which are an important source of carrion for marten during winter (Nagorsen et al. 1991; Carlson et al. 2014). Abandoned roads provide easier pathways for movement than complex forest floors and provide greater cover from aerial predators than openings. Therefore, I hypothesized that marten would avoid areas with high densities of maintained roads and occur more frequently in areas with limited amounts of abandoned roads (Shirk et al. 2012). I measured the density of active and abandoned roads within 100-m and 1000-m distances from each station (Digital Road Atlas, DataBC Distribution Service).

Forest edges function as important habitat for early-seral prey species, such as deer, and provide seasonally-available berries important for marten diet (Ben-David et al. 1997; Côté et al. 2004). Thus, I hypothesized that marten on Haida Gwaii would select home-ranges with greater amounts of edge habitat; however, I expected marten to avoid areas with high density of forest edge when interior forest habitat became limiting (Baker 1992; Shirk et al. 2012). I used the average height of leading tree species estimated from VRI to derive an index of forest edge density. I reclassified the height raster into two height classes, ≥ and <3 m, and interpreted the intersect of the two height classes to be the forest edge (Wilsey et al. 2012). I calculated the mean density of lines of forest edge within 100-m and 1000-m distances from each station. All spatial data were re-projected as raster images with a 20x20-m resolution (ArcMap, version 10.5.1, Environmental Systems Research Institute, Redlands, CA).

I used mixed-effects logistic regression (logit link and a binomial error family) to test for a statistical relationship between the occurrence of marten at camera stations with the combination of sampling and environmental variables that served as model hypotheses (Table 2)

(Pearce & Ferrier 2000). Station ID served as a random effect (i.e., intercept) to control for lack of independence between multiple marten detections at the same trap station (Hebblewhite & Merrill 2007; Tweedy et al. 2019). I used two-term quadratic functions to represent nonlinear relationships between marten detections and independent variables (Purcell et al. 2009). I checked for excessive multicollinearity among covariates; only one model had an average variance inflation factor (VIF) score >2 (Menard 2002). The 'Camera Station Density' model had a VIF score of 2.25, likely because station density and station clustering were both included in that model, and both were metrics of spatial autocorrelation among camera stations.

I used the Akaike Information Criterion adjusted for small sample sizes (AIC_c) to select the models with the greatest support (Anderson et al. 2000; Burnham et al. 2011). I used the ΔAIC_c values to rank models and considered all models with ΔAIC_c <2 as equally likely hypotheses given the data (Burnham et al. 2011). I included the null model as a competing model.

I used a jackknifed (one-at-a-time) cross-validation procedure to test the predictive ability of the most well-supported models (Pearce & Ferrier 2000). I sequentially withheld data from each camera station during model-fitting and then used the resulting model and the withheld records for that station to generate independent predictions. I then compared the independent predictions to the observed data from the withheld camera. I used the receiver operating characteristic (ROC) and the area under the curve (AUC) metric to assess the performance of each model (Fielding & Bell 1997). AUC values >0.8 indicate high predictive accuracy (Manel et al. 2002). I used coefficients from the most well-supported models to predict the mean probability of detection with 95% confidence intervals at specific intervals across the observed

range of values for select covariates, keeping all other covariates at their mean values (margins command in STATA).

Results

Camera stations (n = 72) were deployed across a range of habitat types (Appendix A, Table A1). The average age of leading-tree species measured from VRI data (100-m scale) ranged from 36.6–408.0 years ($\bar{x}$ = 166.6 years, SD = 117.9 years). The average height of trees derived from LiDAR data (100-m scale) ranged from 2.9–22.0 m height ($\bar{x}$ = 14.4 m, SD = 3.7 m). Values of canopy cover measured from LiDAR data (100-m scale) ranged from 34.6–100.0% ($\bar{x}$ = 83.9 m, SD = 15.8 m) and near-ground cover (between 0–1 m height) derived from LiDAR data (100-m scale) ranged from 90.8–100.0% ($\bar{x}$ = 97.0%, SD = 2.2%). Stations were located between 0.0–15.0 km ($\bar{x}$ = 6.4 km, SD = 4.7 km) distance to marine shorelines and between 0.0–2.3 km ($\bar{x}$ = 0.5 km, SD = 0.4 km) distance to riparian areas, measured at the 100-m scale. The proportion of area within 100-m of stations that had been harvested for timber in the past 30 years ranged from 0.0–100.0% ($\bar{x}$ = 6.6%, SD = 19.1%). The density of forest edges and roads at the 100-m scale ranged from 0.0–7.3 km/km^2 ($\bar{x}$ = 1.6 km/km^2, SD = 1.7 km/km^2) and 0–4 km/km^2 ($\bar{x}$ = 1.7 km/km^2, SD = 1.0 km/km^2), respectively.

Each of the 72 camera stations sampled an average of 7.5 (SD = 1; range = 5–9) 2-week intervals. Camera deployment and monitoring over two winters (2017–2018) resulted in 6,786 trap nights that represented 537 2-week sampling intervals. In total, these 2-week intervals represented 158 discrete detections of Pacific marten; a detection rate of 29%. There were 220 2-week sampling intervals and 51 detections in 2017, compared to 317 intervals and 107 detections in 2018.

The information theoretic approach provided support for four models, which accounted for approximately 54% of the variation in the model set (Table 3). More complicated models with greater numbers of parameters were not selected as the most informative for predicting marten detections (Appendix A, Table A2). The four competing (ΔAIC_c <2), nearly equally supported models were from the human disturbance, sampling bias, and topography explanatory categories (Table 3).

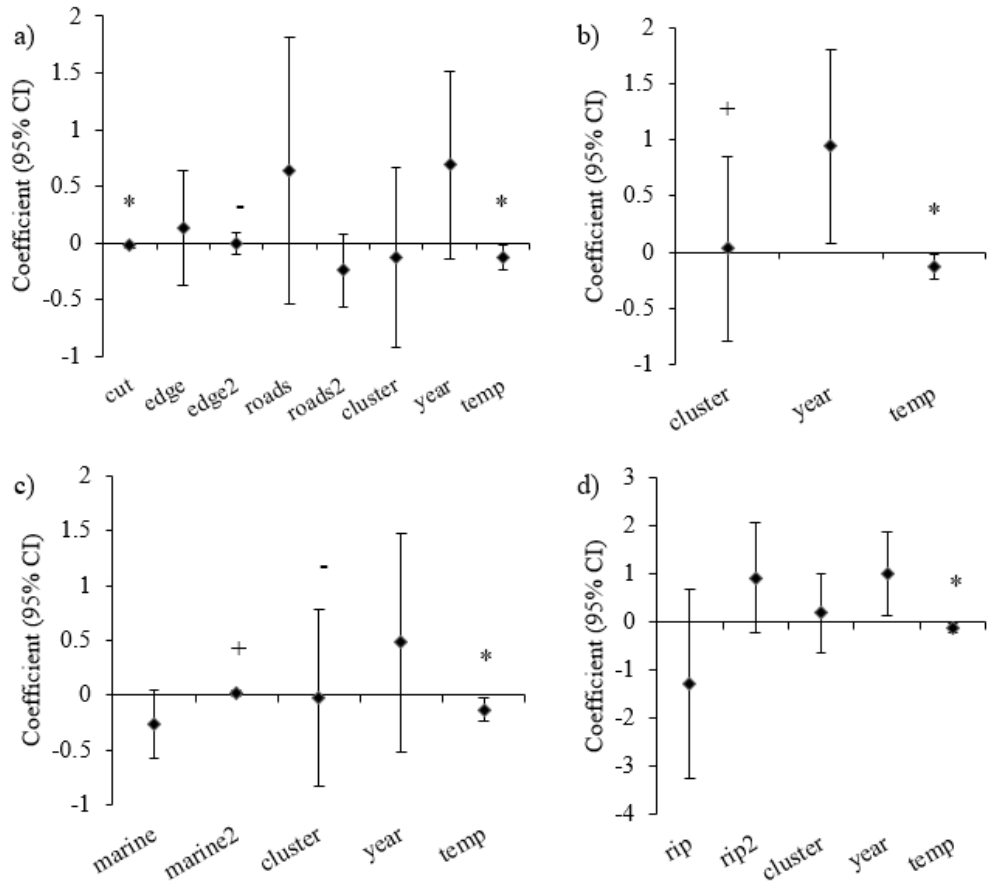
Although there was some model selection uncertainty, the model with the greatest support included covariates representing metrics of human disturbance measured at the 100-m scale (AIC_c w_i = 0.208). That model was highly predictive of the presence of marten at trap stations (AUC = 0.806, SE = 0.021; Table 3). The sampling bias model was the second most well-supported of the full model set (AIC_c, w_i = 0.159; Table 3). That model also had excellent predictive success (AUC = 0.827, SE = 0.019). A topographic model representing distance to marine shoreline, measured at the 100-m scale, was ranked third among competing models (AIC_c w_i = 0.094; Table 3). That model also was an excellent predictor of the distribution of marten across the study area (AUC = 0.822, SE = 0.019). The model for distance to riparian area, measured at the 100-m scale, was the fourth and final competing model (Table 3). That model accounted for 8% of the total AIC_c weight (w_i) and had high predictive accuracy (AUC = 0.823, SE = 0.019).

The human disturbance model included the percent area harvested within 30 years of sampling, as well as quadratic terms for both forest edge density and road density. The percent of total area harvested was negatively correlated with detections of marten (β = -0.023, SE = 0.011, P = 0.041; Figure 2.a, “cut”). As the percent of area harvested increased from 0–50% the predicted probability of detection decreased from 0.307–0.136 (Figure 3.a).

Table 3. Summary of model selection statistics for the most well-supported models ($\Delta AIC_c \leq 2$) of Pacific marten detections at trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada; null model is included for comparison and was not among the most parsimonious models; therefore, predictive ability (AUC) was not calculated. Fixed effects used in logistic regression models are defined in Tables 1 and 2.

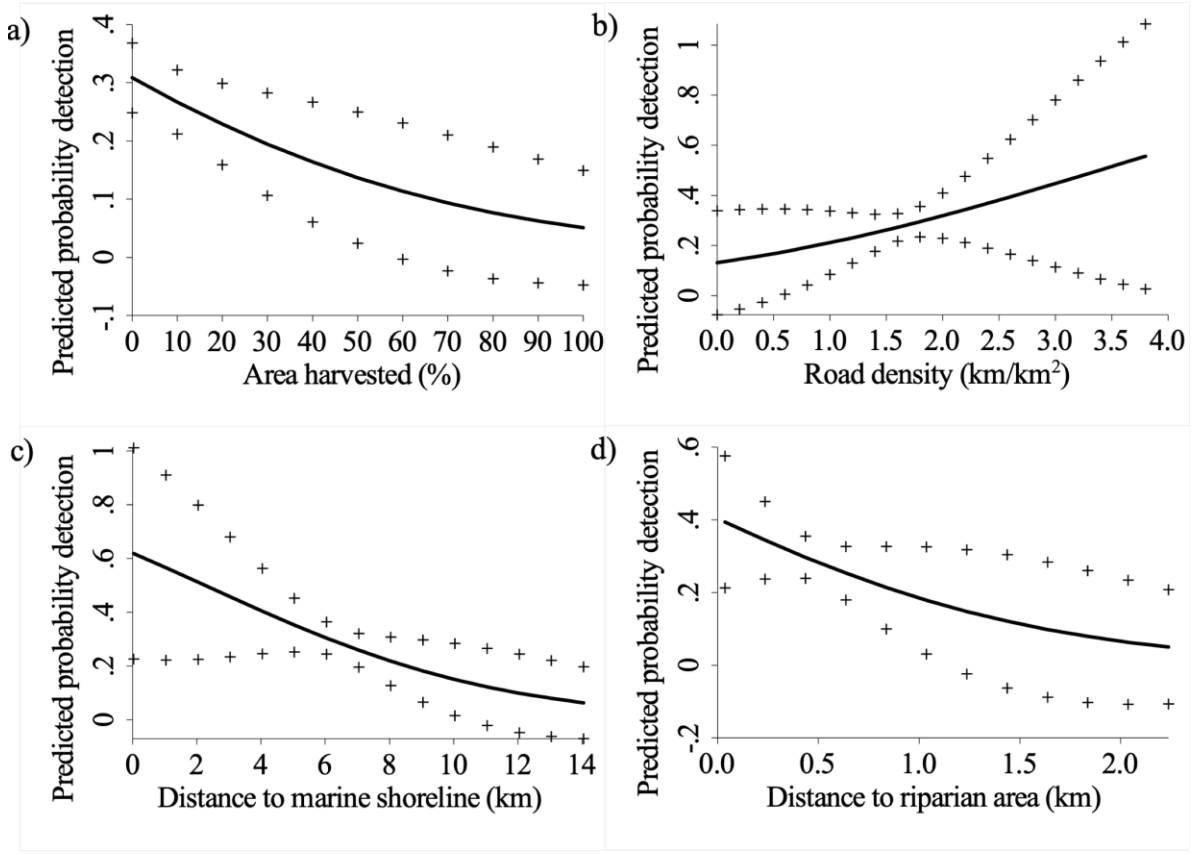
Rank	Logistic Regression Model (scale)	k	AIC_c	ΔAIC_c	AIC_c w_i	AUC
1	Area cut + Forest edge density ^{q} + Road density ^{q} + Station clustering + Year of sampling + Average temperature (100-m)	10	617.810	0.000	0.208	0.806
2	Station clustering + Year of sampling + Average temperature (aspatial)	5	618.347	0.537	0.159	0.827
3	Distance to marine shoreline ^{q} + Station clustering + Year of sampling + Average temperature (100-m)	7	619.398	1.588	0.094	0.822
4	Distance to riparian area ^{q} + Station clustering + Year of sampling + Average temperature (100-m)	7	619.661	1.850	0.083	0.823
12	Null model (intercept with no covariates)	2	621.82	4.007	0.028	–

^{q} indicates two-term quadratic functions.



* denotes statistically significant coefficient ($P < 0.05$)
+ and – signs denote positive and negative coefficients, respectively.

Figure 2. Coefficients with 95% confidence intervals (CI) for fixed effects in the most parsimonious mixed-effects logistic regression models ($\Delta AIC_c \leq 2$) explaining Pacific marten detections across trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, during winters of 2017 and 2018: a) Area harvested, forest edge, and road density; b) Sampling bias; c) Distance to marine shoreline; d) Distance to riparian area. Labels of fixed effects have been shortened and are defined in text as well as in Table 1.



+ indicate 95% confidence intervals (CI).

Figure 3. Predicted probability of detecting Pacific marten at trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, during winters of 2017 and 2018, calculated from changes in predictor variables from the most well-supported logistic regression models, with all other model parameters held at their mean values.

Marten detections were positively correlated with density of forest edge (β = 0.131, SE = 0.258, P = 0.612; Figure 2.a, "edge"). As edge density increased from 0–5 km/km^2 predicted probability of detection increased from 0.247–0.357. However, the relationship between detections and edge density became negative at greater amounts of forest edge (β = -0.010, SE = 0.048; P = 0.833; Figure 2.a, "edge2"). Similarly, there was a nonlinear relationship between detections and density of roads. Marten detections were positively correlated with density of roads (β = 0.641, SE = 0.601, P = 0.287; Figure 2.a, "roads"). When road density increased from 1–3 km/km^2 the predicted probability of detection increased from 0.207–0.453 (Figure 3.b). However, the relationship was likely asymptotic and became negative at greater densities (β = -0.244, SE = 0.162, P = 0.131; Figure 2.a, "roads2").

The sampling bias model included station clustering, year of sampling, and temperature. There was a positive relationship between station clustering and marten detections, but that relationship was not statistically significant (β = 0.028, SE = 0.417, P = 0.946; Figure 2.b, "cluster"). There was a significant, positive relationship between year of sampling and marten detections (β = 0.942, SE = 0.443, P = 0.033; Figure 2.b, "year"). There was a significant, negative relationship between temperature and marten detections (β = -0.134, SE = 0.055, P = 0.015; Figure 2.b, "temp"). As the temperature increased from -2.5–7.7°C the predicted probability of detection decreased from 0.528–0.128.

The two topographic models included distance to marine shoreline and distance to riparian area. There was a nonlinear relationship between marten detections and distance to marine shoreline. Marten detections were negatively correlated with distance to marine shoreline (β = -0.269, SE = 0.161, P = 0.099; Figure 2.c, "marine"). As distance to marine shoreline

increased from 1–10 km the predicted probability of detection decreased from 0.568–0.147 (Figure 3.c). However, at greater distances the relationship between marten detections and distance to marine shorelines became positive (β = 0.019, SE = 0.012, P = 0.135; Figure 2.c, "marine2"). Similarly, there was a nonlinear relationship between marten detections and distance to riparian area. Detections were negatively correlated with distance to riparian area (β = -1.282, SE = 1.010, P = 0.198; Figure 2.d, "rip"). As distance to riparian area increased from 0–1 km the predicted probability of detection decreased from 0.390–0.179 (Figure 3.d). However, the relationship became positive at greater distances from riparian areas (β = 0.910, SE = 0.579, P = 0.116; Figure 2.d, "rip2").

Discussion

I employed remote-camera stations and mixed-effects logistic regression modelling to predict patterns of habitat use of an insular population of marten on Haida Gwaii. The most well-supported models from the set I analyzed contained habitat metrics for human disturbance and topography. Relationships between detections and covariates from the top models suggest that marten on Haida Gwaii were more likely to use habitat with decreased percent area in clearcuts and greater density of forest edge, as well as habitat that is relatively close to streams and marine shorelines. These results are consistent with previous research demonstrating that it is primarily prey abundance and availability, not forest structure or age, that drive patterns of marten distribution (Vigeant-Langlois & Desrochers 2011; Eriksson et al. 2019).

The human disturbance model measured at the 100-m scale was the most informative for explaining patterns of detections of Pacific marten at trap stations in this study. In particular, marten were less likely to be detected in areas with a relatively greater proportion of young forest associated with clear-cut logging – a negative relationship that has been observed for other

coastal populations of the species (Baker 1992; Slauson et al. 2007; Shirk et al. 2014). Marten require downed wood and near-ground structures that are usually absent from regenerating clearcuts (Sherburne & Bissonette 1994; Cushman et al. 2011; Shirk et al. 2014). A number of prey species for marten on Haida Gwaii, including Hairy Woodpecker (*Picoides villosus picoides*) and Red-breasted Sapsucker (*Sphyrapicus ruber*), are much less abundant in clearcuts compared to unharvested forests (Savard et al. 2000; Nagorsen 2006).

Surprisingly, density of roads, including active and abandoned roads, and forest edges were both positively correlated with marten detections. Marten in North America generally avoid roads and forest edges due to increased predation risk and lower availability of preferred prey (Moriarty et al. 2011, 2015; Joyce 2018). However, high edge density likely coincides with the patchwork of clearcuts and old-growth stands that provides forage and cover for deer, an important source of carrion for marten during winter (Nagorsen et al. 1991; Gaston et al. 2002; Côté et al. 2004). Also, marten on Haida Gwaii have very few natural predators and rates of commercial trapping are low; thus, roads and forest edges do not have considerably higher risk of mortality relative to forest interiors (Todd et al. 2018). Marten may benefit from abundant prey associated with greater edge density and face no increase in risk of predation or harvest mortality (Koehler & Hornocker 1977; Spencer et al. 1983; Hargis et al. 1999).

Marten were more likely to be detected near marine shorelines, including at camera stations directly adjacent to the supralittoral zone. Lack of persisting snowpack in forests along marine shorelines may result in more energy-efficient foraging; small mammals that overwinter in subnivean spaces are less accessible than prey found above the surface (Bull 2000). Further, marten may exploit allochthonous food sources in the intertidal zone. Haida Gwaii marten have unique cranial morphology that may be an evolutionary adaptation for crushing the calcareous

shells of marine invertebrates (Foster 1963; Giannico & Nagorsen 1989). Mink (*Neovison vison*), a typically aquatic mustelid, are absent on Haida Gwaii (Foster 1963; Golumbia 2000); thus marten may experience relatively low competition for marine invertebrates (Hodder et al. 2017).

Similarly, the predicted probability of detecting marten decreased the farther stations were from riparian areas. Fish-bearing streams on Haida Gwaii are surrounded by reserve zones where timber harvesting is restricted (Haida Gwaii Management Council & Province of British Columbia 2007). Management and reserve zones are in place to recruit and maintain mature forests within riparian areas, which in turn serve as foraging and resting habitat for marten and other forest specialists (Spencer et al. 1983; Buskirk et al. 1989; Shirk et al. 2014). Furthermore, salmonid fish scavenged from other predators are an important source of food for marten during fall and winter in coastal areas (Nagorsen et al. 1991; Ben-David et al. 1997). Reserve zones that protect riparian forests from logging, combined with seasonally-abundant salmon, likely contribute to the selection of riparian areas by marten on Haida Gwaii (Haida Gwaii Management Council & Province of British Columbia 2007).

The model designed to test sampling bias in data collection was among the most informative for explaining patterns of marten detections. A positive response to bait may have contributed to the increase in detection rate from 2017–2018. Marten that had encountered baited stations in 2017 may have been more likely to visit stations that were accessible in 2018. I replenished bait and re-applied lure more frequently in 2018 than in 2017, which may have increased the probability of detection (Sirén et al. 2016). However, patterns in marten detections likely represent underlying habitat heterogeneity more than variability in the amount or frequency of baiting (Stewart et al. 2019).

Average temperature at trap stations was negatively correlated with marten detections. Temperatures at trap stations never dropped below -10°C. In similar climates of the Pacific Northwest, nocturnal temperature in winter is not low enough to result in thermoregulatory behavior, thus, activity patterns typically do not differ between the midwinter months and early spring (Zielinski et al. 1983). Seasonal patterns in activity of coastal marten may be more influenced by fluctuations in prey availability and juvenile dispersal (Zielinski et al. 1983). Marten are resource limited in winter and home-ranges expand in size, which may increase the probability of detection (Zielinski et al. 2009). During winter, marten may shift home-ranges to include marine shorelines as foraging habitat, as is observed in other endemic carnivores on Haida Gwaii (Waterhouse et al. 2017). As more resources become available in the spring, home-ranges contract, resulting in fewer marten detections (Ben-David et al. 1997; Zielinski et al. 2015). Transient juveniles detected during winter dispersal from maternal home-ranges may also contribute to increased detections in midwinter, relative to the spring (Zielinski et al. 2009, 2015).

Models of forest structure were not among the most well-supported of the set I analyzed (Appendix A, Table A2), and no coefficients associated with structural metrics were statistically significant (Appendix A, Table A3). Lack of correlation between forest structure and marten detections was not due to a lack of variability in forest structural metrics among stations (Appendix A, Table A1). Forest structure, such as coarse woody debris, canopy complexity and cover appear to be less important to marten on Haida Gwaii when compared to other populations in North America (Soutiere 1979; Spencer et al. 1983; Delheimer et al. 2019). This may be due to the maritime climate, high availability of prey, lack of competition, and a low risk of predation.

Structural complexity associated with unlogged old forests provides subnivean access to resting sites in areas of high snowfall (Thompson & Colgan 1994; Shirk et al. 2014). The thermal properties of downed wood make them important resting sites for marten in regions with very cold winters (Buskirk et al. 1989; Corn & Raphael 1992). On Haida Gwaii, however, there is relatively little annual snowfall and no persisting snowpack at low elevations (Banner et al. 2014). The lowest temperature at camera stations during the sampling period was -8°C. Therefore, subnivean resting sites associated with old-forest structures may not be a requisite component of habitats used during winter by marten in the area that I sampled.

Patterns of marten distribution depend on the availability of preferred prey (Spencer et al. 1983; Baker 1992; Payer & Harrison 2003). The diet of marten in interior regions of North America is dominated by voles, a species associated with structurally complex forests (Poole et al. 2004; Eriksson et al. 2019). However, voles are absent from Haida Gwaii and marten there, as in other coastal areas, are considered dietary generalists (Ben-David et al. 1997; Eriksson et al. 2019; Manlick et al. 2019). Subnivean access associated with structural complexity is likely less important for marten foraging on Haida Gwaii relative to regions where voles are present (Sherburne & Bissonette 1994; Thompson & Colgan 1994). Use of habitat for foraging is probably associated with increased prey activity regardless of forest age (Keim et al. 2011; Vigeant-Langlois & Desrochers 2011).

The four most well-supported models accounted for approximately half of the variation of the model set ($\sum AIC_c\ w_i = 0.544$; Table 3). Therefore, there was considerable uncertainty in my estimation of model support (Burnham et al. 2011). The sampling bias model was among the best explanatory models (Table 3). The null model, which contained only the random variable for camera station ID and no fixed-effects, accounted for more variation in the model set than

three competing models for human disturbance and forest structure (Appendix A, Table A2). These results suggest that there were other factors influencing marten distribution that I did not include in the model set. Those potential covariates likely occurred at a scale of habitat that I did not measure, including the percent cover and species composition of understory herbaceous shrubs, the size and number of standing live and dead trees, the size, decay-class, and number of pieces of woody debris, and relative prey availability (Eriksson et al. 2019; Delheimer et al. 2019). Further, marten were not detected at 14 camera stations, and the detection rate across stations was low (29%) based on expected high density of marten in the study area. Marten were likely present in sampling units, but were not detected, leading to misclassification of photo data. Misclassification of the response variable can increase uncertainty in model selection and reduce the predictive accuracy of models.

The jackknife, leave-one-out approach to model validation suggested high predictive accuracy for the top models (AUC >0.8; Table 3). Using this approach, I withheld data from one camera station at a time to generate predicted detections and subsequently compared predictions to observed detections from the withheld camera. This method may have resulted in overestimation of predictive accuracy. Therefore, results from the top models should not be generalized to predict marten distribution in areas outside the sample units of this study. Rather, the top models provide new insight into patterns of marten habitat use in an intensively managed area of Haida Gwaii and add to the current knowledge of the plasticity in habitat ecology among coastal populations of Pacific marten in North America.

American and Pacific marten are considered old forest specialists due to the assumed reliance on structurally complex forests for denning, foraging, and avoiding predators (but see Baker 1992; Poole et al. 2004; Vigeant-Langlois & Desrochers 2011; Eriksson et al. 2019).

However, marten on Haida Gwaii showed no affinity for structural complexity and were more likely to be detected in areas with optimum densities of roads and forest edges. This relationship likely reflects the importance of forest edges as foraging habitat for marten on Haida Gwaii, and suggests habitat use strategies locally adapted to the altered foodscape, most importantly the reliance on carrion from introduced deer during winter (Spencer et al. 1983; Nagorsen et al. 1991).

This is the first study to demonstrate the importance of marine shoreline as habitat for Pacific marten. The diet of Pacific marten in coastal areas includes fish and marine invertebrates, and marten in this study were active in the upper intertidal and supralittoral zones (Ben-David et al. 1997; Nagorsen 2006). Preference for forests at the land-ocean interface is likely facilitated by a lack of competition and relatively little predation risk, and further differentiates the habitat ecology of marten on Haida Gwaii from other coastal populations.

Management implications

Marten generally occur at low densities across North America and are the focus of reintroduction efforts where populations have been extirpated due to habitat loss and over-trapping (Schorger 1942; Manlick et al. 2017; Linnell et al. 2018). Information about the distribution and patterns of habitat use of marten is vital for their effective conservation and management. Pacific and American marten are generally considered to be habitat specialists of late-seral forests (Soutiere 1979; Buskirk 1984; Slauson et al. 2007). Late-seral forests are characterized by complex horizontal and vertical structure which provides sites for resting and denning, and supports high densities of preferred prey (Spencer et al. 1983; Mowat 2006; Delheimer et al. 2019).

Marten function as an indicator, or focal species for management, due to their reliance on structurally complex old forests that function as habitat for other species of conservation concern (Wasserman et al. 2012; Lavoie et al. 2019). However, the most well-supported models from the set I analyzed contained habitat metrics for human disturbance and topography, rather than forest structure. These results emphasize that the importance of forest structure for populations of generalist mesocarnivores such as Pacific marten, depends on the landscape and ecological context in which they occur (Wasserman et al. 2012; Moriarty et al. 2016a; Eriksson et al. 2019).

Relationships between detections and covariates from the top models suggest that marten on Haida Gwaii were more likely to use habitat with decreased percent area in clearcuts, greater amounts of forest edge and roads, as well as habitat that was relatively close to streams and marine shorelines. These results confirm that marten and other mustelids in North America are less likely to use young stands where logging has occurred, due to the removal of structures that are necessary for survival, as well as decreases in the abundance of prey (Lavoie et al. 2019; Suffice et al. 2019). I found a negative relationship between the probability of marten detection and the proportion of area that had been harvested for timber in the past 30 years within 100-m of camera stations (3 ha circular area). These findings suggest that old forests should be retained in unharvested patches at least 0.03 km^2 (3 ha) in order to increase the probability of fine-scale habitat use by Pacific marten. Forest edges and roadsides may function as foraging habitat for marten when diet is composed mainly of edge species, and there is low risk of mortality from predation or trapping.

Marten were more likely to use habitat closer to marine shorelines; however, distance to marine shoreline could not be used to accurately predict habitat use at distances >10 km. Similarly, marten were more likely to use habitat closer to riparian areas, and distance to riparian

areas was not an accurate predictor of habitat use at distances >1 km. Forests bordering rivers and marine shorelines may contain greater shrub cover, and support greater numbers of small mammals and birds than forests located farther from water (Spencer et al. 1983; Shirk et al. 2012; Eriksson et al. 2019). Similar habitat associates have been observed among competing populations of endemic Haida ermine (*Mustela erminea haidarum*; Reid et al. 2000). Intraguild competition is likely high between marten and ermine in riparian forests compared to other habitats. Similarly, the Saw-whet Owl (*Aegolius acadicus brooksi*) forages for amphipods in the marine intertidal, and nests primarily in old-growth forests (Hobson & Sealy 1991; Waterhouse et al. 2017). Forested shorelines should be protected from harvest and development in order to provide adequate amounts of foraging habitat for competing species of native and endemic carnivores.

The unique habitat ecology of marten on Haida Gwaii has implications for conservation planning for species at risk found across this remote, but relatively disturbed archipelago (Reid et al. 2000; Manlick et al. 2019). Marten are an apex predator in the ecological context of Haida Gwaii and likely play a role in regulating faunal communities directly through predation and competition, as well as indirectly through trophic cascades (Crooks & Soulé 1999; Golumbia 2000; Ritchie & Johnson 2009). Based on overlap in distribution and habitat use, intraguild competition and predation from marten may regulate populations of several species at risk, most notably the coastal subspecies of Northern Goshawk, the endemic subspecies of Northern Saw-whet Owl, and the endemic Haida ermine (Reid et al. 2000; Waterhouse et al. 2017). The use of habitat by Pacific marten should be considered in ecosystem-based management of forest values and ecological processes, as well as strategic planning for the recovery of populations of forest specialists that are endemic to this uniquely altered and globally rare old-forest ecosystem.

Chapter 3: Using stable-isotope analysis to investigate spatial and temporal variability in the diet of Pacific marten on Haida Gwaii

Introduction

Mesocarnivores, including marten (*Martes* spp.), occupy different ecological niches depending on climate, competition, predation, and prey availability (Golumbia 2000; Roemer et al. 2009; Ritchie & Johnson 2009). When compared to continental populations of North America, Pacific marten (*Martes caurina*) from island ecosystems have greater niche breadth, show a higher degree of dietary plasticity, and can function as apex predators (Nagorsen et al. 1991; Manlick et al. 2019). The diets of coastal island populations of marten fluctuate seasonally with the abundance of the small number of species of small mammals present, the timing of salmon spawning events, periods of bird migration and nesting, fruiting periods for understory plants, and periods of high mortality of deer (*Odocoileus* spp.; Ben-David et al. 1997; Carlson et al. 2014; Twining et al. 2019).

The Pacific marten is one of only three species of carnivore native to the Haida Gwaii archipelago. The abundance of marten on Haida Gwaii, British Columbia (BC), appears to have increased in the last century, possibly due to the favorable combination of abundant resources and little competition or predation from other carnivores (Reid et al. 2000). Introduced mammal species, including Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), beaver (*Castor canadensis leucodontus*), muskrat (*Ondatra zibethicus osoyoosensis*), red squirrel (*Taimasciurus hudsonicus lanuginosus*), black rat (*Rattus rattus*), and house mice (*Mus musculus*) have all been found to contribute to the diet of Pacific marten on Haida Gwaii (Nagorsen et al. 1991; Nagorsen 2006). The recent increase in diversity and availability of prey, most notably deer carrion from hunter- and winter-kills, may increase the carrying capacity of the landscape for marten (Reid et

al. 2000; Carlson et al. 2014; Todd et al. 2018). There is also evidence that marten on Haida Gwaii consume approximately equal proportions of marine organisms, berries, and terrestrial vertebrates (Manlick et al. 2019). Access to marine allochthonous nutrients can contribute to higher densities of generalist carnivores in foreshore habitats relative to inland (Rose & Polis 1998; Eriksson et al. 2019).

Past research used the contents of gastrointestinal (GI) tracts to quantify the diet of marten on Haida Gwaii during the winter, when the species is typically commercially trapped (Nagorsen et al. 1991; Nagorsen 2006). Morphological analysis of GI tracts requires lethal sampling, often over-represents diet items that are resistant to digestion, and provides dietary information for relatively short time periods (Cumberland et al. 2001; Darimont & Reimchen 2002; Slauson & Zielinski 2017). Recently, stable-isotopes of carbon (C) and nitrogen (N) have been used to quantify the diet of marten on Haida Gwaii during the fall (Manlick et al. 2019).

Stable-isotopes are forms of the same element that differ in number of neutrons, and hence atomic mass, and physical processes lead to variation in the ratios of heavy to light isotopes in organic compounds (Ben-David & Flaherty 2012). In diet studies, isotopic signatures of predators result from assimilation of nutrients from consumed prey (Hobson et al. 1997). Discrimination is the process of differential assimilation of heavy and light isotopes by consumer tissues relative to ingested food sources. The process varies with many ecological and physiological factors, including trophic level, metabolic rate, and excretion (Phillips et al. 2014).

Differential fixation of light carbon isotopes during photosynthesis occurs between C3 and C4/CAM plants and results in different ^{13}C to ^{12}C isotope ratios that are preserved with little discrimination at higher trophic levels (DeNiro & Epstein 1978; Ben-David & Flaherty 2012). Consumers preferentially assimilate the heavier ^{15}N (nitrogen) isotope and excrete the lighter

^{14}N, resulting in greater ratios of ^{15}N to ^{14}N at higher trophic levels, a process referred to as trophic enrichment (Post 2002; Ben-David & Flaherty 2012; Milakovic & Parker 2013).

Within an individual consumer, differences in isotopic signatures between tissues can be used to infer diet at the time the tissue was grown, and compare diet between different time periods (Hilderbrand et al. 1996). Isotopic signatures of hair represent assimilation over the growth period, while assimilated nutrients can remain in bone collagen for decades (Hobson et al. 1997; Darimont & Reimchen 2002). In contrast, muscle and red blood cells turn over every 70–80 days, and blood plasma and liver cells turn over every 1–10 days (Hilderbrand et al. 1996; Milakovic & Parker 2011).

The functional role of marten in coastal temperate rainforests may depend on seasonal fluctuations in prey availability, access to marine resources, including salmon and marine invertebrates, and may change depending on sex, age, and nutritional condition (Nagorsen et al. 1991; Ben-David et al. 1997; Slauson & Zielinski 2017). The generalist foraging behavior of marten has implications for the conservation of insular populations of endemic species on Haida Gwaii (Edie 2001; Cooper et al. 2004; COSEWIC 2006, 2013). Marten may outcompete other native species for shared resources and limit recovery of species at risk through intraguild predation (Polis & Holt 1989; Hobson & Sealy 1991; Reid et al. 2000). Effective conservation strategies for the ecosystems of Haida Gwaii require further knowledge of the foraging ecology and diet of Pacific marten, and the implications for at-risk prey species and their associated trophic dynamics.

My research objectives were to use stable-isotopes of carbon and nitrogen to: 1) estimate relative contributions of different food sources to marten diet across seasons and during overall lifetime; 2) determine how diet varies with different levels of access to marine resources,

including salmon and marine invertebrates; and 3) investigate differences in diet by sex, age and nutritional condition. I hypothesized that marten diets would vary seasonally with availability of prey. I expected diets to be most enriched in both $\delta^{13}C$ and $\delta^{15}N$ in the fall, when salmon carcasses were most abundant (Ben-David et al. 1997). I expected that signatures would become more depleted as time since salmon spawning events increased (Darimont & Reimchen 2002). Further, I hypothesized that marten would consume relatively greater amounts of salmon in areas with greater access to salmon-bearing streams (Ben-David et al. 1997). Similarly, I hypothesized that marten located close to marine shorelines would have relatively greater dietary contributions from marine invertebrates (Nagorsen et al. 1991; Manlick et al. 2019).

Methods

Study Area

Haida Gwaii is a remote archipelago located approximately 50–130 km offshore from mainland BC and southeast Alaska (Banner et al. 2014; Figure 4). The archipelago is approximately 10,000 km^2 in area and is comprised of two main islands, Graham Island and Moresby Island (Gaston et al. 2002). Forests covering the landmass are mostly old-growth coniferous temperate rainforests with salal (*Gaultheria shallon*) and several species of *Vaccinium* in the understory. Like most island ecosystems, the vertebrate community of Haida Gwaii is depauperate relative to the adjacent mainland (Foster 1963; Gaston et al. 2002). The only large predator is the omnivorous Haida Gwaii black bear (*Ursus Americanus carlottae*), and there are no canid or felid predators other than feral dogs and cats in forests adjacent to towns (Gaston et al. 2002). The mesocarnivore community consists only of river otter (*Lontra canadensis*), Pacific marten, and the endemic Haida ermine (*Mustela erminea haidarum*) (Foster 1963). Introduced raccoons (*Procyon lotor vancouverensis*) are common (Golumbia 2000).

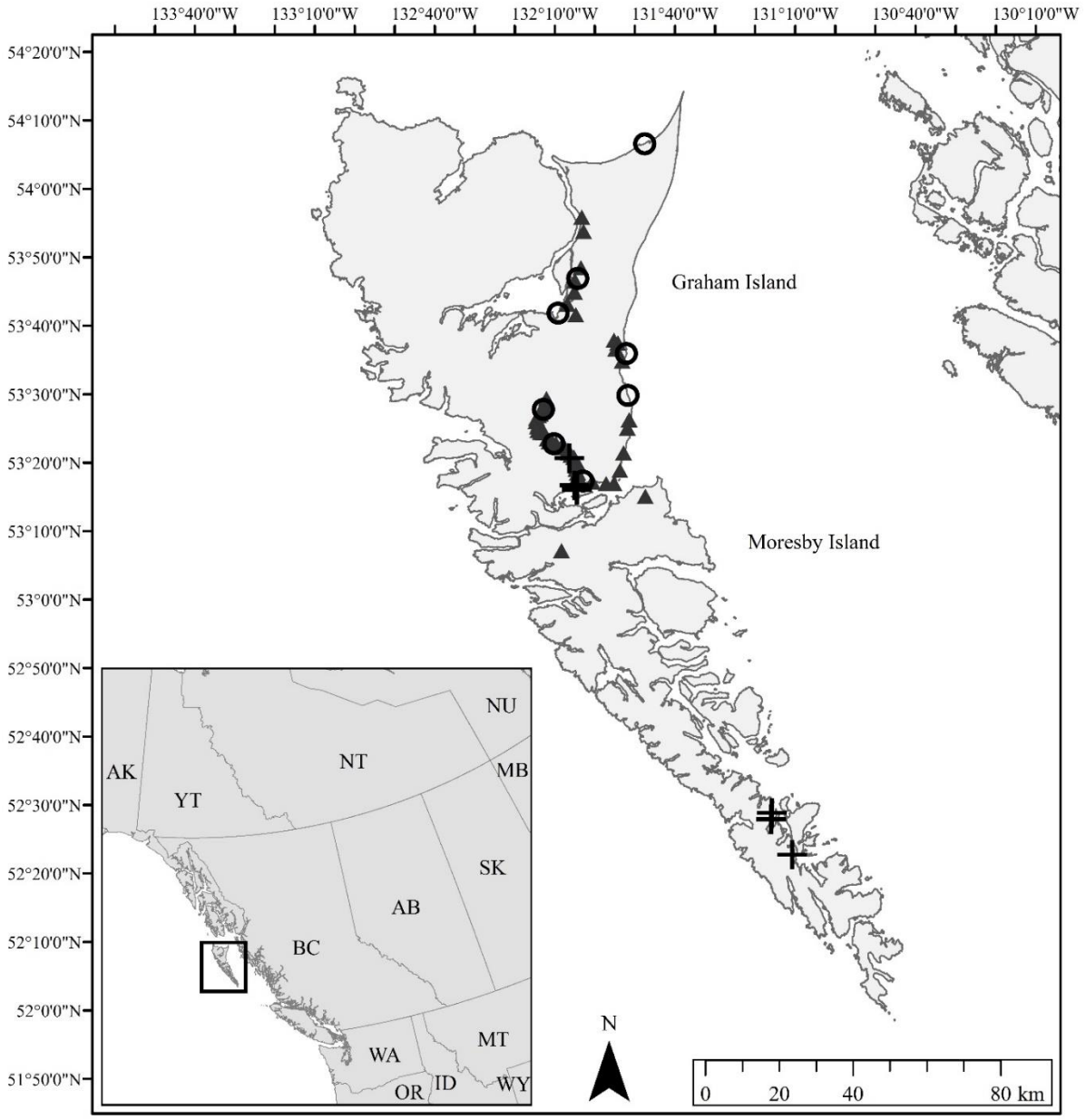


Figure 4. Sampling locations for Pacific marten on Haida Gwaii, British Columbia, Canada between 2013–2018. Grey triangles represent locations of marten collected from traplines and roadkill (n = 122), and black crosses represent locations of hair snares and live-trapping (n = 8). Small mammals and terrestrial and marine invertebrates were collected from eight locations (open circles) between February 15–September 6, 2016.

Historically, the only native species of large herbivore was the Dawson's caribou (*Rangifer tarandus dawsoni*), now extinct (circa 1920-1930); European red deer (*Cervus elaphus elaphus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and Sitka black-tailed deer were all introduced in the late 19th and early 20th century to provide hunting opportunities (Gaston et al. 2002). The native rodent community consists only of Keen's mouse (*Peromyscus keeni*), of which there are two subspecies. However, introduced beaver, muskrat, red squirrel, black rat, Norway rat (*Rattus norvegicus*), and house mice are now widespread (Golumbia 2000; Government of Canada Public Services and Procurement Canada 2002). Other than four species of bats, the only other mammal species native to the islands is the dusky shrew (*Sorex monticolus*), of which there are two subspecies (Gaston et al. 2002).

Likewise, the avifaunal and reptile communities are less diverse than on the adjacent mainland (Savard et al. 2000; Government of Canada Public Services and Procurement Canada 2002). Most of the predators on Haida Gwaii are resident birds of prey, including Bald Eagle (*Haliaeetos leucocephalus*), Red-tailed Hawk (*Buteo jamaicensis*), Northern Goshawk (*Accipiter gentilis laingi*), Sharp-shinned Hawk (*Accipiter striatus*), Peregrine Falcon (*Falco peregrinus*), and an endemic subspecies of Northern Saw-whet Owl (*Aegolius acadicus brooksi*; British Columbia 2004). Picides are limited to Red-breasted Sapsucker (*Sphyrapicus ruber*), the endemic subspecies of Hairy Woodpecker (*Picoides villosus picoides*), and Northern Flicker (*Colaptes auratus*; Savard et al. 2000). Migrating passerine birds occur seasonally, and Sooty Grouse (*Dendragapus fuliginosus*) are the only species of gallinaceous bird native to the islands (Banner et al. 2014). There are no reptiles and the only native amphibian is the western toad (*Anaxyrus boreas*); however, Pacific tree frog (*Pseudacris regilla* and northern red-legged frog (*Rana aurora*) have been introduced and are widespread (Gaston et al. 2002).

Sampling

I used carbon and nitrogen stable-isotope ratios of hair and tissue samples from Pacific martens (n = 130) collected from registered traplines, roadkill, live-traps, and baited hair snares between 2013–2018 (Figure 4; Appendix B, Table B1). Guard hair, bone and muscle samples were collected from trapped and road-killed martens (n = 122), while guard hair was collected from individual martens caught by live-traps and hair snares (n = 8). During the necropsy of trapped and road-killed martens (n = 122), marten age class (adult or juvenile <1 year) was estimated from temporal muscle coalescence and confirmed from cementum annuli (Appendix B, Table B1; Todd et al. 2016). Nutritional condition was assessed based on subcutaneous and internal fat deposits using a modified five-class descriptive scale adapted from the four-class system of Hatler et al. 2003 (Poole et al. 1994; Todd et al. 2016; Kirby et al. 2018).

I used stable-isotope signatures of tissues that differed in assimilation period to evaluate seasonal variability in diet (Hilderbrand et al. 1996). Bone collagen takes decades to replace, thus the isotopic signature reflects assimilated lifetime diet (Schwertl et al. 2003). Contrastingly, muscle represents diet assimilated during a two- to three-month period (Milakovic & Parker 2013). Therefore, muscle from marten collected between December and February (n = 104) approximated diet assimilated between September and February (Hilderbrand et al. 1996; Milakovic & Parker 2011). Growth of winter pelage begins in July and is complete by mid-October (Pauli et al. 2009). Guard hairs were cut into distal and proximal sections (relative to the root), to estimate diet assimilated during summer and early fall, respectively (Appendix B, Table B1; Darimont et al. 2008).

Diet items previously reported in Pacific marten diet on Haida Gwaii or elsewhere in North America were collected to establish baseline isotopic signatures (Breault & Phillips 2016).

Most marten diet samples of mammals, birds, and fish were donated by the Haida Gwaii community from animals killed by road, cats, and licenced hunters and anglers between 2005–2018. I collected berries, terrestrial and marine invertebrates, and Keen's mice from six sampling locations on Graham Island as part of a provincial government research team between February 15–September 6, 2016 (Todd et al. 2018). I used baited snap traps to collect Keen's mice. I set invertebrate pitfall traps, with propylene glycol and water solution (1:1) to trap and preserve terrestrial invertebrate specimens and conducted shoreline searches to collect a suite of marine invertebrate taxa. Metabolically active muscle tissue samples were collected from vertebrate specimens and were stored frozen, along with whole invertebrate and plant specimens. Most collection locations were close to the source locations of winter-trapped or road-killed marten and varied in proximity to marine shorelines to include terrestrial fauna with a broad range of marine isotopic signatures (Figure 4; Ben-David et al. 1998).

All marten and vertebrate diet item tissues and whole specimens of invertebrates and berries were freeze-dried or oven-dried (60°C), then ground by mortar and pestle to achieve homogeneity. Depending on the isotope (C or N), between 0.5–5 mg of the sample was transferred to a tin capsule. Marten hair samples were cleaned of surface oils using repeated rinses of a 2:1 chloroform: methanol solution, and then dried in an oven at 60°C overnight. Hair (0.2–0.8 mg) was cut and placed into tin cups (Hobson et al. 2000; Fry 2007).

Total nitrogen and carbon isotope compositions were determined using a thermal combustion elemental analyzer (EA) (*Costech ECS 4010*, Costech Analytical Instruments Inc., Valencia, CA) coupled via a flow-reducing interface (ConFlow III) with a continuous flow isotope ratio mass spectrometer (IRMS) (*Thermo Finnigan Delta^{PLUS} Advantage*, ThermoFinnigan Inc., Bremen, Germany). Nitrogen and carbon isotope data are reported in δ-

notation in units of per mil (‰) with reference to atmospheric nitrogen (air) and Vienna Pee Dee Belemnite (VPDB) carbonate, respectively. Two types of secondary reference material in duplicates were analyzed before and after each batch of samples: dorm with $\delta^{13}C$, $\delta^{15}N$ values of -17.17 ‰ and 14.33 ‰, respectively, and caffeine with $\delta^{13}C$, $\delta^{15}N$ values of -42.02 ‰ and -0.95 ‰, respectively. This study was approved by the Animal Care and Use Committee, University of Northern British Columbia (Protocol Number: 2017-09) and conducted under the authority of the British Columbia (BC) Ministry of Forests, Lands, Natural Resource Operations, and Rural Development and an approved BC Animal Care Application.

Data analysis

Marten on Haida Gwaii consume a broad range of diet items compared to marten in other regions of North America (Nagorsen et al. 1991; Manlick et al. 2017, 2019). Typically, mixing models are limited to $n + 1$ sources, where n equals the number of isotopes; therefore, three groups of diet items would be the maximum number of sources to avoid underdetermination in mixing models based on $\delta^{13}C$ and $\delta^{15}N$ (Phillips et al. 2014). However, the Stable-Isotope Analysis (SIAR) package (Parnell & Jackson 2015) incorporates uncertainty in source isotope values, as well as fractionation correction factors, and can give reliable estimates in underdetermined models (Parnell et al. 2010; Carlson et al. 2014). Therefore, I limited the number of diet items to four, in order to increase diet resolution while maintaining model reliability (Kirby et al. 2018). I performed all statistical analyses in R Studio (version 1.1.456, RStudio Inc., Boston, MA).

I included diet items previously reported in marten diet in North America that could be separated into distinct groups based on ecosystem, taxonomy, and isotopic signature (Appendix B, Table B2; Breault & Phillips 2016). Models included: salmon, including Chinook

(*Oncorhynchus tshawytscha*), Chum (*Oncorhynchus keta*), and Coho (*Oncorhynchus kisutch*); marine invertebrates, including amphipods, crabs, marine snails, and blue mussels (*Mytilus edulis*); birds, including Sooty Grouse, Red Crossbill (*Loxia curvirostra*), Fox Sparrow (*Passerella iliaca*), Song Sparrow (*Melospiza melodia*), Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*Catharus guttatus*), Varied Thrush (*Ixoreus naevius*), American Robin (*Turdus migratorius*), Brown Creeper (*Certhia americana*), Orange-crowned Warbler (*Vermivora celata*), Townsend's Warbler (*Setophaga townsendi*), Golden-crowned Kinglet (*Regulus satrapa*), Pacific Wren (*Troglodytes pacificus*), Red-breasted Sapsucker, Hairy Woodpecker, and Northern Flicker; mammals, including red squirrel, Sitka black-tailed deer, muskrat, Keen's mouse, both species of rat, and dusky shrew; terrestrial ground beetles (Carabidae); and berries from salal and red huckleberry (*Vaccinium parviflorum*; Appendix B, Table B2).

For all comparisons of $\delta^{13}C$ and $\delta^{15}N$ among groups of diet items and marten, I tested for violations of assumptions of normality (Shapiro-Wilk test) and equal variances (F-test). When assumptions were met, I proceeded to test for significant differences in $\delta^{13}C$ and $\delta^{15}N$ between unpaired groups using Pearson's t-test. When assumptions were violated, I used a Kruskal-Wallis test with a Tukey-Kramer post-hoc test of multiple comparisons for unpaired data, and a Wilcoxon signed-rank test with a Bonferroni post-hoc test for evaluating differences among groups of paired data.

I plotted values of $\delta^{13}C$ and $\delta^{15}N$ for each diet item before grouping them into taxonomic categories (Appendix B, B2). I used a Kruskal-Wallis test with a Tukey-Kramer post-hoc test to evaluate separation among items. Based on the results of this analysis and model limitations, I combined diet items into four primary groups: salmon, marine invertebrates, terrestrial fauna

(beetles, mammals, and birds), and berries (Appendix B, Table B1). I used a weighted mean to average the isotopic contribution of each diet item within the terrestrial fauna category. I derived the weights (w_i) from the relative importance of each item to the diet of marten on Haida Gwaii as observed from analyses of contents of GI tracts: $w_1 = 0.3$ for deer and insectivorous birds (all birds except grouse), $w_2 = 0.06$ for grouse and small mammals (squirrel, muskrat, Keen's mouse, rat, and shrew), and $w_3 = 0.04$ for beetles (Nagorsen et al. 1991). Prey sampling occurred throughout the year; therefore, I used a Kruskal-Wallis test with a Tukey-Kramer post-hoc test to compare isotope signatures among four seasons within each diet group (Appendix B, Table B3).

I corrected diet item $\delta^{13}C$ and $\delta^{15}N$ using trophic enrichment factors (TEF) developed during captive feeding experiments on mink and black bears (Ben-David 1996; Hilderbrand et al. 1996) (Appendix B, Table B4). I applied TEFs of +2‰ to $\delta^{13}C$ of terrestrial fauna and berries, +1‰ to $\delta^{13}C$ of salmon and marine invertebrates, +3‰ to $\delta^{15}N$ of terrestrial fauna, marine invertebrates, and berries, and +2‰ to $\delta^{15}N$ of salmon (Appendix B, Table B4). These TEFs have been used to successfully correct isotope values for similar diet items in stable-isotope analyses of marten diet in Alaska (Ben-David et al. 1997).

I used Bayesian isotopic mixing models in SIAR to estimate relative proportions of diet items in marten diet (Parnell et al. 2010; Parnell & Jackson 2015). SIAR allows concentration dependence and this accounts for differences in carbon and nitrogen concentrations between diet items (Phillips & Koch 2002; Appendix B, Table B4). All models used a uniform prior Dirichlet distribution, with 500,000 iterations and a burn-in of 10%.

I performed a Wilcoxon signed-rank test with Bonferroni correction to test for significant differences in $\delta^{13}C$ and $\delta^{15}N$ between marten tissue types. I evaluated seasonal variability in diet by comparing mean and 95% Bayesian credibility intervals (BCI) among tissue types: distal

guard hair (n = 121), proximal guard hair (n = 121), muscle (n = 104), and bone (n = 122). I included data points for hair only if they came from marten sampled between November and June, inclusive, which is outside the growth period for marten guard hair (Markley & Bassett 1942; Soutiere & Steventon 1981; Pauli et al. 2009). Assuming marten grow hair at a constant rate, distal guard hair represents diet assimilated between July and August (summer), and proximal guard hair represents diet assimilated between September and October (fall). Similarly, I only included data points for muscle from marten sampled between December and February, inclusive. This represents diet assimilated between September and February (fall and winter), a time period which overlaps with salmon spawning events (Hobson et al. 1997).

Consumers with a diet consisting of marine resources have isotope signatures that are naturally enriched in $\delta^{13}C$ and $\delta^{15}N$ (Ben-David et al. 1997; Darimont & Reimchen 2002). A strong linear relationship between $\delta^{13}C$ and $\delta^{15}N$ indicates consumption of marine-derived resources including salmon and marine invertebrates (Pauli et al. 2012). I performed ordinary least squares regression to determine if $\delta^{13}C$ could be used to predict $\delta^{15}N$. I tested for a linear relationship between time, as represented by the number of days since the beginning of the sampling period (December 3rd), and $\delta^{13}C$ and $\delta^{15}N$ derived from the muscle of sampled marten.

I used isotope values from proximal guard hair sections to compare fall diet among marten (n = 121) sampled in areas with different densities of salmon-bearing streams. I calculated the line density of salmon-bearing streams within 1 km of each marten collection location (from BC fish observations, BC Fish Distributions, Stream Centreline Network, DataBC Distribution Service) in ArcMap (GIS; ArcMap, version 10.5.1, Environmental Systems Research Institute, Redlands, CA). I grouped marten based on the 1st and 3rd quartiles of the

sample of stream densities: low (≤0.22 km/km^2, n = 35), medium (>0.22 km/km^2 and ≤0.60 km/km^2, n = 53), and high (>0.60 km/km^2, n = 33).

I used isotope values from bone to compare lifetime diet among marten (n = 122) sampled at three distances to marine shorelines. I grouped marten based on the 1st and 3rd quartiles of the distances of sampled marten from marine shorelines: near (≤2.6 km, n = 26), moderately close (>2.6 and ≤10.7 km, n = 67), and far (>10.7 km, n = 29). I used a Kruskal-Wallis test with a Tukey-Kramer post-hoc test to determine differences in isotope values among marten from different distances.

I used isotope values from proximal guard hair sections to compare fall diet between young of the year (n = 52) and adults (n = 57). I performed an unpaired two-sample t-test to determine if the mean $\delta^{13}C$ and $\delta^{15}N$ values from proximal guard hair sections were significantly different between age classes. I used confirmed age from cementum annuli when available and otherwise I used age estimated during necropsy (Appendix B, Table B1; Todd et al. 2016). Similarly, I used isotope values from proximal guard hair sections (n = 120) to examine differences in diet estimates between females (n = 47) and males (n = 73). Finally, I used a Kruskal-Wallis test with a Tukey-Kramer post-hoc test to determine if $\delta^{13}C$ and $\delta^{15}N$ values of bone (n = 121) were significantly different between marten assigned to two categories of nutritional condition: Poor, Fair, & Good (n = 69), and Excellent & Obese (n = 52).

Results

Most diet items were significantly different from each other in at least one isotope signature (P <0.05; Figure 5). Exceptions were beetle and deer, which overlapped in both $\delta^{13}C$ and $\delta^{15}N$ values. Likewise, shrew, insectivorous birds (Figure 5, "i.bird"), and Keen's mouse

(Figure 5, "k.mouse") overlapped in both $\delta^{13}C$ and $\delta^{15}N$ values. Isotope values of muskrat were not significantly different from other diet items, probably due to low sample size (n = 2). The four primary diet item groups (salmon, marine invertebrate, terrestrial fauna, and berry) included in mixing models were all significantly different from each other in both isotopes (Figure 6; Appendix B, Table B1). Isotope values were stable between seasons within all groups except berries (Figure 7; Appendix B, Table B3). Berries differed significantly in $\delta^{13}C$ among seasons, a reflection of seasonal differences in the composition of species sampled rather than seasonal changes in isotope signatures: winter and spring samples contained only salal, summer contained only red huckleberry, and fall contained salal, oval-leaf blueberry, and red huckleberry.

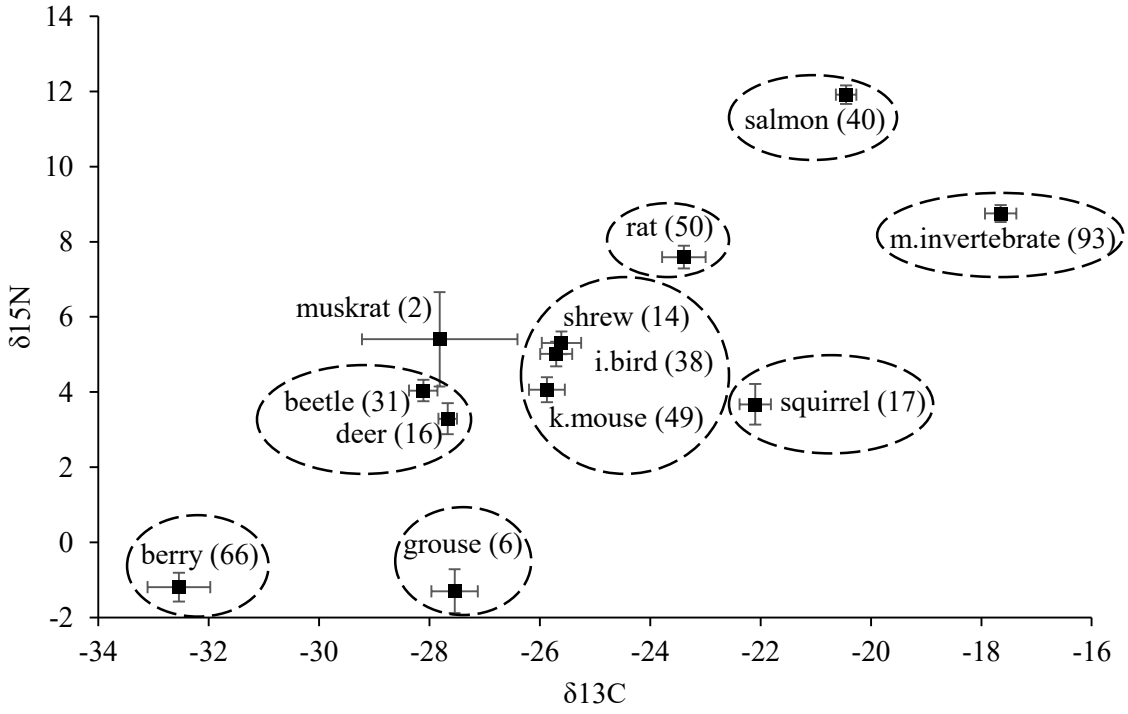


Figure 5. Values of $\delta^{13}C$ and $\delta^{15}N$ ($\bar{x} \pm 95\%$ CI) for each diet group (labelled with sample size) collected on Haida Gwaii, British Columbia, Canada, between 2005–2018, uncorrected for trophic fractionation. Dashed lines indicate groups were significantly different from all other groups in at least one isotope signature ($P < 0.05$).

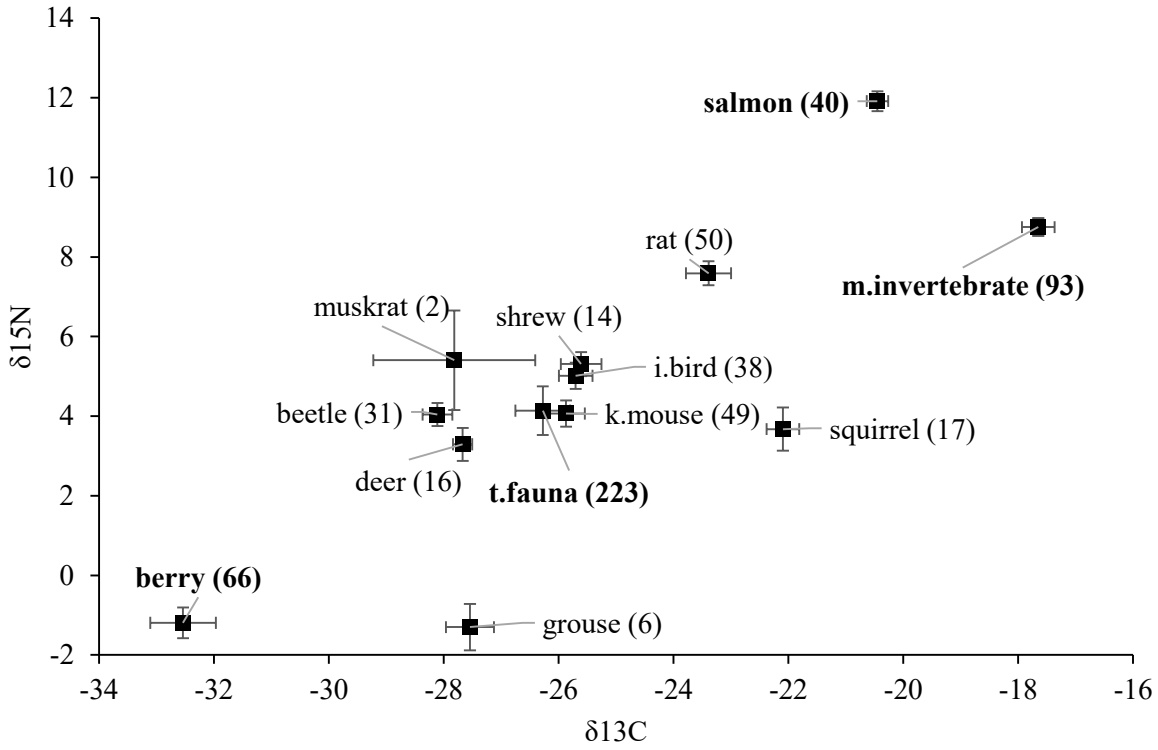


Figure 6. $\delta^{13}C$ and $\delta^{15}N$ ($\bar{x} \pm 95\%$ CI) for each diet group (with sample size) collected on Haida Gwaii, British Columbia, Canada, between 2005–2018, uncorrected for trophic fractionation. Diet groups with bold labels were used in mixing models. The mean values of $\delta^{13}C$ and $\delta^{15}N$ for terrestrial fauna (t.fauna) were calculated from weighted averages based on previous diet studies.

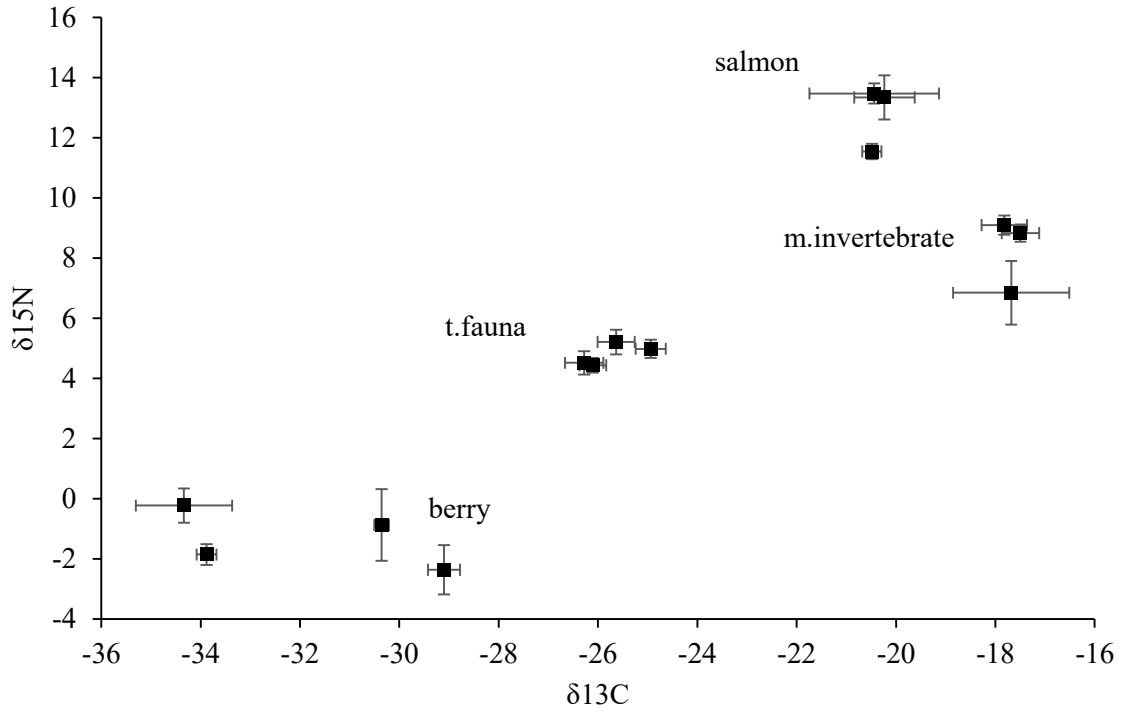


Figure 7. $\delta^{13}C$ and $\delta^{15}N$ values of diet items ($\bar{x} \pm SE$) by season collected on Haida Gwaii, British Columbia, Canada, between 2005–2018. Berry includes salal and red huckleberry; t.fauna includes weighted averages of the mean $\delta^{13}C$ and $\delta^{15}N$ values of birds, mammals, and beetles; salmon includes Chinook, Coho, and Chum; and marine invertebrate (m.invertebrate) includes amphipods, crabs, and gastropods.

Values of $\delta^{13}C$ and $\delta^{15}N$ for individual Pacific marten fell within the range of $\delta^{13}C$ and $\delta^{15}N$ values of diet items after correction for trophic enrichment (Figure 8). Therefore, it was possible to use Bayesian mixing models to estimate solutions to diet composition (Phillips et al. 2014). All tissue types were significantly different in $\delta^{13}C$ values ($P < 0.05$) and bone was significantly different in $\delta^{15}N$ from all other tissues ($P < 0.001$; Figure 9). There were no significant differences in $\delta^{15}N$ between other tissues ($P > 0.05$). Relative proportions estimated from bone suggested that terrestrial fauna and marine invertebrates contributed most to lifetime diet (49–57% and 41–48%, respectively), whereas berries (0–3%) and salmon (0–3%) contributed relatively little (Figure 10; Table 4). However, diet estimates from other tissues suggested that berries and salmon were important seasonally (Figure 10; Table 4).

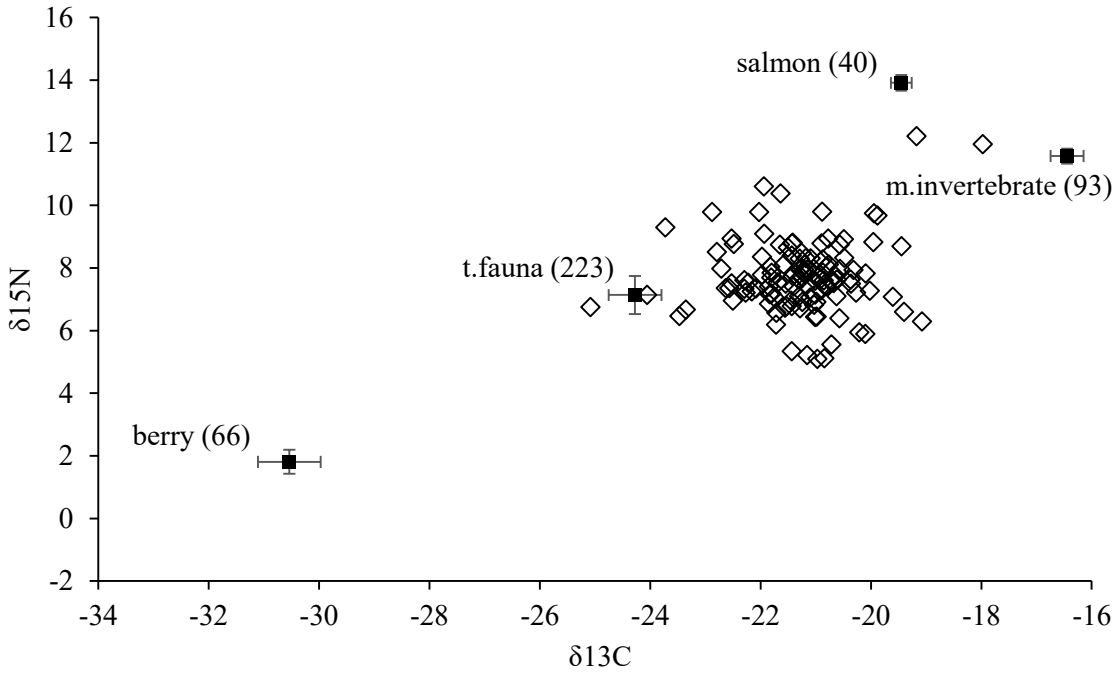


Figure 8. $\delta^{13}C$ and $\delta^{15}N$ values ($\bar{x} \pm SE$) of diet groups (black squares) corrected for trophic enrichment, as well as isotope values of Pacific marten bone (open diamonds, $n = 122$) for comparison. Diet items were collected between 2005–2018, and marten were sampled between 2013–2018, on Haida Gwaii, British Columbia, Canada.

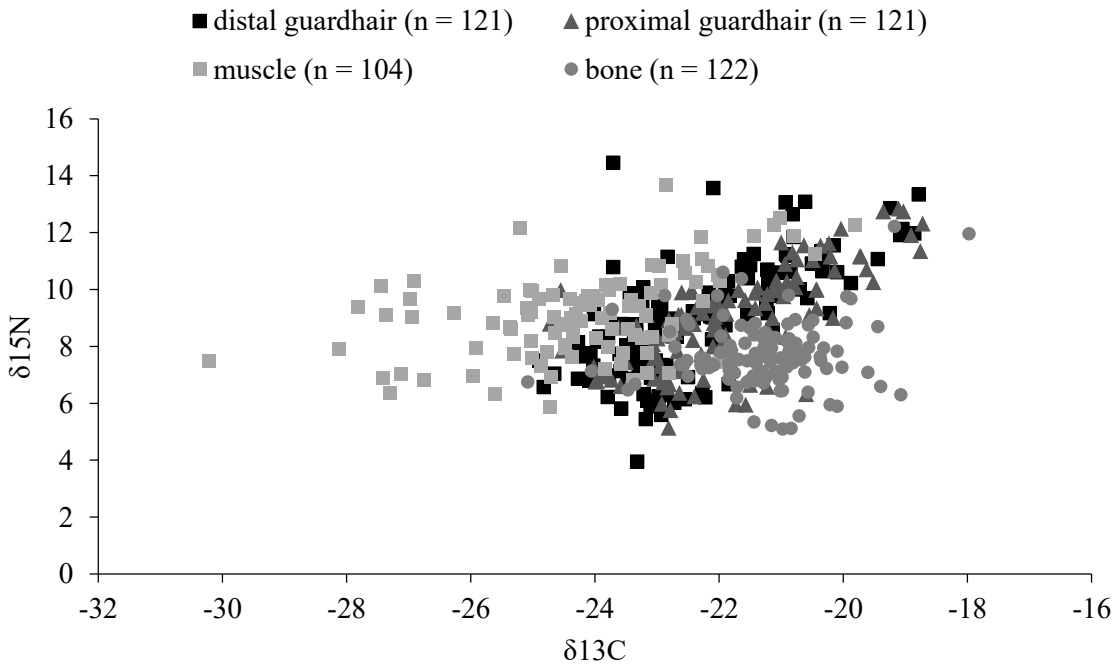


Figure 9. $\delta^{13}C$ and $\delta^{15}N$ values for individual Pacific marten collected on Haida Gwaii, British Columbia, Canada, between 2013–2018, symbolized by tissue type: distal guard hair, proximal guard hair, muscle, and bone.

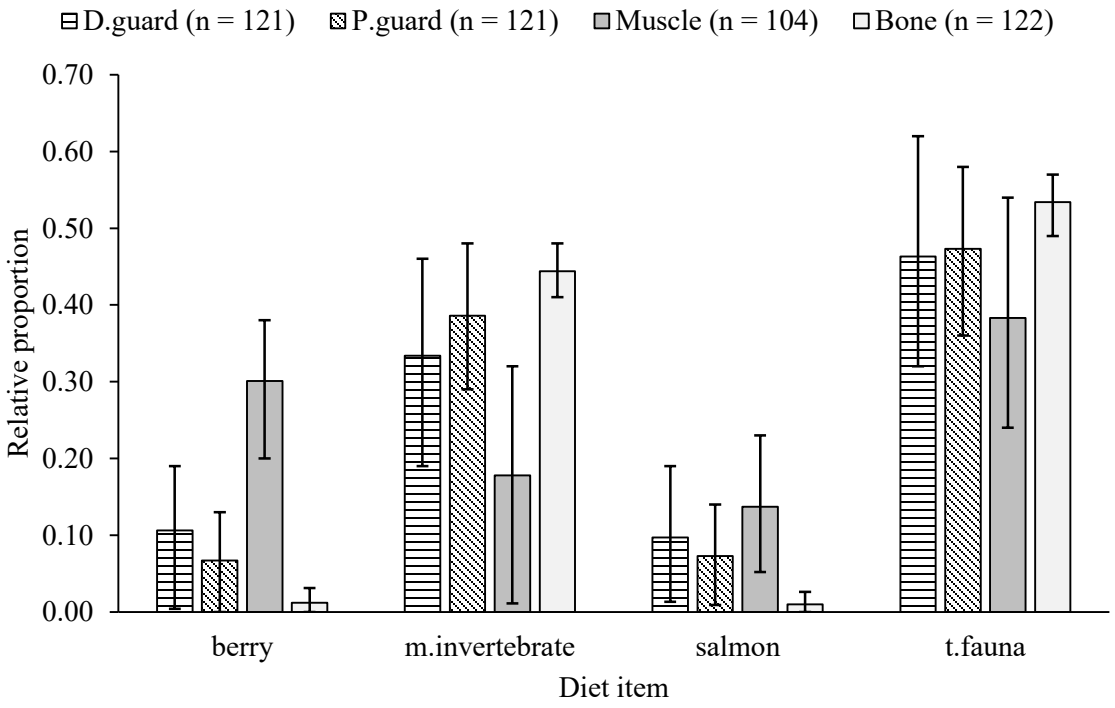


Figure 10. Relative proportions ($\bar{x}$ ± 95% CI) of diet items in Pacific marten diet by tissue type, estimated using Bayesian stable-isotope mixing models. Diet items were collected between 2005–2018, and marten were collected between 2013–2018, on Haida Gwaii, British Columbia, Canada.

Table 4. Relative proportions ($\bar{x}$ ± 95% CI) of diet items in Pacific marten diet by consumer category (*n*), estimated using Bayesian stable-isotope mixing models. Diet items were collected between 2005–2018, and marten were collected between 2013–2018, on Haida Gwaii, British Columbia, Canada.

	Mean (95% CI)			
Consumer categories (*n*)	**berry**	**m.invertebrate**	**salmon**	**t.fauna**
Tissue type				
Distal guard hair (*n* = 121)	10.6 (0.4–19)	33.4 (19–46)	9.7 (1.3–19)	46.3 (32–62)
Proximal guard hair (*n* = 121)	6.7 (0–13)	38.6 (29–48)	7.3 (0.9–14)	47.3 (36–58)
Muscle (*n* = 104)	30.1 (20–38)	17.8 (1.1–32)	13.7 (5.2–23)	38.3 (24–54)
Bone (*n* = 122)	1.2 (0–3.1)	44.4 (41–48)	1 (0–2.6)	53.4 (49–57)
Salmon density (p.guard)				
≤ 0.22 km/km^2 (*n* = 35)	5.9 (0–14)	37.2 (26–47)	4.4 (0–11)	52.6 (38–65)
0.22–0.60 km/km^2 (*n* = 53)	9.3 (0–18)	36.9 (22–51)	11.7 (1.6–22)	42.1 (28–57)
≥ 0.60 km/km^2 (*n* = 33)	6.6 (0–15)	38.6 (26–51)	8.8 (0.3–18)	45.9 (33–58)
Distance to marine (bone)				
≤ 2.6 km (*n* = 26)	3.1 (0–8.1)	43.2 (35–51)	2.7 (0–7.1)	50.9 (42–60)
2.6–10.7 km (*n* = 67)	1.9 (0–4.8)	44.4 (39–50)	2.2 (0–5.2)	51.5 (46–57)
≥ 10.7 km (*n* = 29)	2.6 (0–7.1)	41.9 (34–49)	1.8 (0–5.1)	53.6 (44–62)
Age class (p.guard)				
Juvenile (*n* = 52)	6.1 (0–13)	42.1 (30–53)	9.6 (1.3–18)	42.2 (31–53)
Adult (*n* = 57)	6.8 (0–14)	30.5 (19–42)	8.3 (0.6–16)	54.4 (41–66)
Sex (p.guard)				
Female (*n* = 47)	4.8 (0–11)	46.3 (36–56)	7.5 (0–15)	41.4 (31–51)
Male (*n* = 73)	6.5 (0–14)	28.5 (17–40)	11.3 (3.5–19)	53.7 (42–65)
Nutritional condition (bone)				
Poor, Fair & Good (*n* = 69)	2 (0–5.1)	44.6 (40–49)	1.8 (0–4.5)	51.6 (46–57)
Excellent & Obese (*n* = 52)	1.8 (0–4.7)	43.1 (38–48)	1.4 (0–3.7)	53.8 (48–59)

Diet estimates generated from muscle tissue showed that between September and February, marten consumed more berries (20–38%) and salmon (5–23%) than at other times of the year (Figure 10; Table 4). Likewise, estimates from distal and proximal guard hair sections (Figure 10, "D.guard" and "P.guard", respectively) showed greater consumption of berries (0–19% and 0–13%, respectively) and salmon (1–19% and 1–14%, respectively) during summer and fall, when those tissues were presumably grown.

Linear regression revealed a significant relationship between $\delta^{13}C$ and $\delta^{15}N$ sampled from the proximal guard hair, indicating a significant marine component to the fall diet ($r^2 = 0.51$, df = 127, $P < 0.001$; Figure 11). Variation in muscle $\delta^{13}C$ and $\delta^{15}N$ values was largely explained by the number of days since the first marten was collected (December 3rd; Figure 12), and there was a significant linear relationship between time and isotope values (for $\delta^{13}C$, $r^2 = 0.07$, df = 88, $P = 0.012$; for $\delta^{15}N$, $r^2 = 0.05$, df = 88, $P = 0.035$), both confirming seasonal changes in diet.

Variation in access to marine resources had only a small influence on the diet of marten (Table 4). Marten that occupied areas with low and medium density of salmon-bearing streams had significantly different $\delta^{15}N$ from each other as measured in the proximal guard hair ($P = 0.016$). Marten from areas with few salmon-bearing streams had the lowest relative contribution of salmon (0–11%) and berries (0–14%), and the greatest relative contribution of terrestrial fauna (38–65%) to the estimated diet. Similarly, there was a significant difference in $\delta^{15}N$ of bone between marten collected at moderate distances and marten collected at far distances from marine shorelines ($P = 0.045$). Marten that were the farthest from marine shorelines had the lowest relative contribution of marine invertebrates (34–49%), and the greatest relative contribution of terrestrial fauna (44–62%; Table 4).

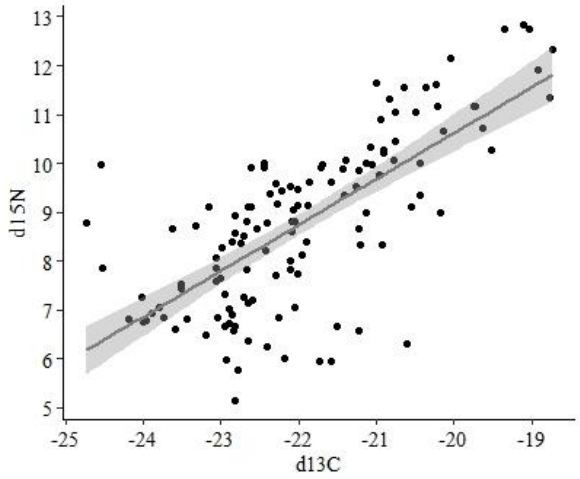


Figure 11. Actual $\delta^{13}C$ and $\delta^{15}N$ values from proximal guard hair sections (n = 130) of Pacific marten with predicted proximal guard hair $\delta^{15}N$ (solid line) from $\delta^{13}C$, with 95% CI (shaded area), calculated from ordinary least-squares regression. Guard hairs were collected from marten between 2013–2018 on Haida Gwaii, British Columbia, Canada.

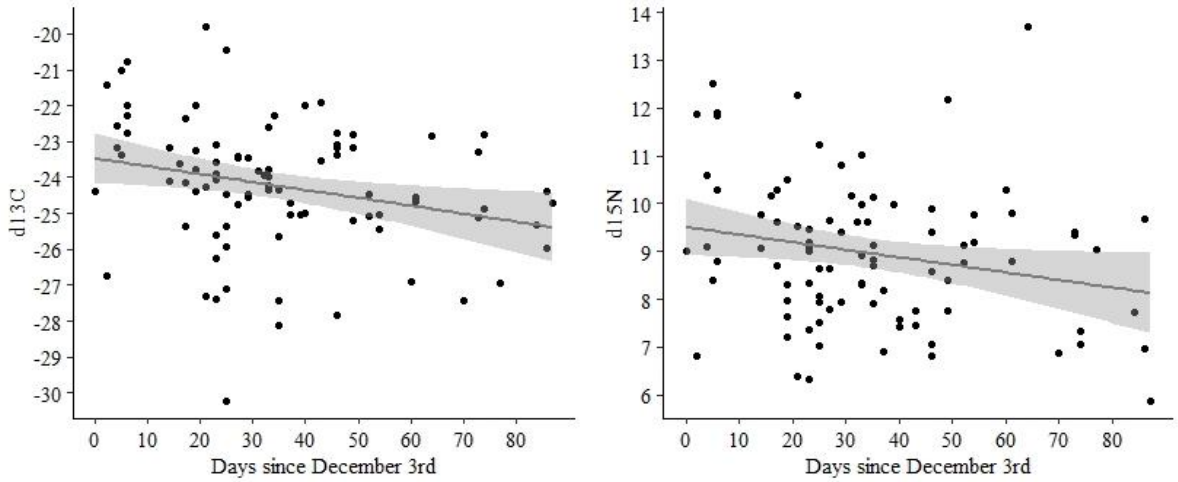


Figure 12. Actual $\delta^{13}C$ and $\delta^{15}N$ values from muscle (n = 90) of Pacific marten, with isotope values predicted (solid line) from time since first marten was sampled (December 3rd), with 95% CI (shaded area), calculated using ordinary least-squares regression. Muscle was collected between 2013–2018 on Haida Gwaii, British Columbia, Canada.

Diet appeared to differ between age classes and sexes during late summer and early fall (Table 4). Both $\delta^{13}C$ and $\delta^{15}N$ values from proximal guard hair sections were significantly different between age classes ($df = 107$, $P < 0.001$ and $P = 0.04$, respectively). The diet of adult marten had a greater relative proportion of terrestrial fauna (41–66%) and less marine invertebrates (19–42%) when compared to juvenile marten. The relative contributions of terrestrial fauna and marine invertebrates were approximately equal (31–53% and 30–53%, respectively) for juvenile marten (Table 4). The relative contribution of berries and salmon were approximately equal for the two age classes. When comparing males and females, the proximal guard hair sections differed significantly in $\delta^{13}C$ ($df = 118$, $P < 0.001$). The relative proportion of marine invertebrates was greater for females (36–56%) than for males (17–40%). Relative proportions of terrestrial fauna, berries, and salmon were all marginally greater for males than for females (Table 4).

Finally, $\delta^{15}N$ of bone was greater for marten in poor, fair, or good nutritional condition, than for marten in excellent or obese condition ($P = 0.02$). However, nutritional condition did not influence the estimates of diet (Table 4).

Discussion

Stable-isotope analyses revealed that terrestrial fauna, including mammals, birds, and beetles, contributed more than any other item to the diet of Pacific marten on Haida Gwaii during all seasons. This is consistent with previous findings that birds and deer carcasses are the most important prey for marten on Haida Gwaii (Nagorsen et al. 1991; Nagorsen 2006). The importance of terrestrial fauna as primary prey is consistent with the hypothesis that increased abundance of marten is due to an influx of introduced terrestrial prey, most notably deer (Reid et al. 2000). The availability of winter-killed deer may improve nutritional condition and survival

during winter, and increase juvenile recruitment (Reid et al. 2000; Carlson et al. 2014; Todd et al. 2018).

Results suggest that marine invertebrates play a larger role in overall lifetime diet for Pacific marten than was thought. Previous stable-isotope analyses of the fall diet of marten on Haida Gwaii estimated roughly equal contributions from marine-derived nutrients, terrestrial vertebrates, and berries (Manlick et al. 2019). Analyses of GI tracts from winter-trapped marten suggested salmon were much more frequently consumed than marine invertebrates (Nagorsen et al. 1991). However, my findings suggest that marine invertebrates, not salmon, are the main allochthonous marine nutrient subsidy to lifetime diet for the marten sampled on Haida Gwaii. I estimated that marine invertebrates contributed slightly less to lifetime diet than terrestrial fauna; salmon and berries were minor components of lifetime diet and were only important seasonally in summer and fall.

I found a significant linear relationship between $\delta^{13}C$ and $\delta^{15}N$ values in proximal guard hair and muscle. Marine-derived food sources are naturally enriched in both $\delta^{13}C$ and $\delta^{15}N$, therefore a strong linear relationship between $\delta^{13}C$ and $\delta^{15}N$ in the consumer sample suggests the diet contains marine-derived nutrients. However, I also found a significant, negative linear relationship between time and isotopic enrichment. The variation in muscle $\delta^{13}C$ and $\delta^{15}N$ was largely explained by time since the peak in availability of salmon during fall runs, represented as the number of days since the first marten was sampled. Depletion of both $\delta^{13}C$ and $\delta^{15}N$ in muscle over time during the winter indicates that intake of marine-derived nutrients was greatest in the fall, the annual spawning season for most species of salmon.

Results from the diet analysis suggest that the relative contribution of marine invertebrates decreased only slightly with increasing distance from marine shorelines (Table 4).

This finding is consistent with the observed movement of genotyped marten identified with hair samples taken from baited hair snares at camera stations deployed on the southern portion of Graham Island (unpublished data, this study). Within a winter season, hair-snagged marten moved a maximum of 12 km Euclidean distance from stations in the supralittoral zone to stations in inland forests. These movement distances are similar to those published in other studies of Pacific marten (Moriarty et al. 2017). Likewise, the relative contribution of salmon to fall diet increased only slightly with increased density of salmon-bearing streams (Table 4).

The stable-isotope mixing models revealed differences in diet between sexes that suggest resource partitioning. I found that the relative contribution of marine invertebrates was greater for female than for male diet (Table 4). Marten on Haida Gwaii are more sexually dimorphic than other coastal populations of Pacific marten (Giannico & Nagorsen 1989), and the difference in body size between male and female marten may reduce intersexual competition for prey (Davies et al. 2007). Greater sexual dimorphism may allow this insular population to occupy a broader dietary niche in the absence of most other mesocarnivores that are sympatric with mainland populations (Giannico & Nagorsen 1989; Nagorsen et al. 1991; Manlick et al. 2017). However, with the exception of marine invertebrates, relative contributions of diet items were only marginally greater for males than for females (Table 4).

Management implications

My findings situate marten within the trophic landscape of Haida Gwaii and further our understanding of the dietary ecology of marten in North America. This study confirms that terrestrial fauna, including birds, deer, and small mammals, are the most important component of diet for marten on Haida Gwaii (Nagorsen et al. 1991; Nagorsen 2006). Marten are one of only three species of mammalian carnivore native to the archipelago; competitors are native black

bear, river otter, and ermine, as well as introduced raccoon (Golumbia 2000; Manlick et al. 2019). Thus, Pacific marten are positioned at a high trophic level with few competitors relative to other parts of their range (Manlick et al. 2017, 2019).

As apex predators, marten may exert strong top-down effects in island ecosystems where the diversity of primary consumers is relatively depauperate (Roemer et al. 2009; Prugh et al. 2009). Marten predation may regulate populations of small mammals and birds, indirectly affecting population dynamics of primary producers (Polis & Holt 1989). Contrastingly, seasonal and interannual fluctuations in the availability and abundance of terrestrial fauna may exert bottom-up control of marten populations. Variability in population density of marten and other mesocarnivores may be strongly correlated with changes in the abundance of vertebrate prey (Roth et al. 2007; Flynn & Schumacher 2009).

Changes in the abundance and distribution of carrion from hunter- and winter-killed deer may affect marten populations directly (Ben-David et al. 1997; Flynn & Schumacher 2009; Carlson et al. 2014). Marten abundance and fecundity are correlated with temporal variability in abundance of preferred prey, likely due to nutritionally-demanding processes associated with reproduction and juvenile recruitment (Flynn & Schumacher 2009; Carlson et al. 2014). Coupling of predator-prey population cycles is more evident when the diversity of prey is low (Roth et al. 2007).

Marten populations may also be regulated by deer indirectly through multitrophic interactions resulting from the effects of overbrowsing of understory vegetation. Forest-dwelling birds may be the most important prey group for marten on islands where the diversity of small mammal communities is low (Nagorsen et al. 1991; Nagorsen 2006). Overbrowsing by deer removes vegetation, as well as associated invertebrates, and reduces habitat quality for forest

songbirds (Allombert et al. 2005a,b). Declines in the abundance and diversity of forest songbirds caused by overbrowsing has resulted in decreased availability of important prey for the threatened population of Northern Goshawk on Haida Gwaii, and potentially increased resource competition between goshawk and marten (Parks Canada 2018).

I provide the first evidence that throughout their lifetime, marten on Haida Gwaii consume relatively high quantities of marine invertebrates (Manlick et al. 2017). The marine intertidal zone provides a consistent source of allochthonous marine nutrients in a region with seasonal fluctuations in most food sources, including birds, mammals, salmon, and berries (Ben-David et al. 1997; Rose & Polis 1998). Marten may use shorelines as foraging habitat in coastal areas of North America where pressure from competition and risk of predation are low (Eriksson et al. 2019). Marten may transport allochthonous nutrients from marine environments and riparian areas to inland forests through the deposition of feces and prey remains. Transportation of marine-derived nutrients can increase primary production in terrestrial ecosystems relative to forests with no marine subsidies, and is an important ecosystem service provided by black bears and river otters (Ben-David et al. 1998; Crait & Ben-David 2007; Quinn et al. 2009). Marten move greater distances than other mammals of similar body size and may provide the same important service in coastal areas (Hickey et al. 1999; Moriarty et al. 2016b, 2017).

Abundant nutrients derived from marine sources can result in higher densities of opportunistic mesocarnivores, including marten, along marine shorelines relative to inland habitats (Moriarty et al. 2016a; Linnell et al. 2018; Eriksson et al. 2019). However, the community-level consequences of this phenomenon are not well understood (Rose & Polis 1998; Roemer et al. 2009). Abundance and availability of marine invertebrates should be considered when assessing the habitat for marten (Rose & Polis 1998; Linnell et al. 2018; Manlick et al.

2019). Further research is needed on the ecology of forest-adapted mesocarnivores located in coastal areas.

Stable-isotope analysis of distal and proximal guard hair sections and muscle tissue suggests salmon and berries are only seasonally important diet items, and provide further evidence that marten in coastal systems vary their diet according to the availability of resources (Baker 1992; Slauson & Zielinski 2017; Eriksson et al. 2019). Dietary plasticity may explain why marten on Haida Gwaii are able to benefit from species introductions while concurrently accommodating considerable alterations to habitat from industrial logging (Gaston et al. 2002; Manlick et al. 2019; Twining et al. 2019). Previous researchers have demonstrated high dietary plasticity among carnivores native to Haida Gwaii. In particular, coastal populations of the endemic subspecies of Northern Saw-whet Owl seasonally forage for amphipods in the marine intertidal (Hobson & Sealy 1991; Waterhouse et al. 2017). This foraging behavior is rare in mainland owl populations and may be the reason Saw-whet Owls are the only resident species of owl on Haida Gwaii (Hobson & Sealy 1991). Similar plasticity in foraging ecology, combined with a broad dietary niche, may allow marten to outcompete other native and endemic carnivores that have more specialized foraging behaviors (Hobson & Sealy 1991; Nagorsen et al. 1991; Reid et al. 2000).

The unique diet ecology of Pacific marten, including reliance on marine invertebrates, as well as seasonal use of salmon and berries, should be considered in strategic planning for the recovery of species at risk on Haida Gwaii. The overlap in dietary niche between marten and other native species of terrestrial vertebrates is likely greater than was determined in previous studies (Hobson & Sealy 1991; Nagorsen et al. 1991; Reid et al. 2000); therefore, marten may regulate vertebrate communities through resource competition (Prugh et al. 2009). For example,

potential interference and exploitative competition with marten have been identified as important factors limiting the recovery of Haida ermine (Edie 2001). The endemic subspecies of ermine likely does not benefit from introduced mammals, including Sitka black-tailed deer, beaver, muskrat, red squirrel, black rat, and Norway rat, which are all important prey for marten on Haida Gwaii during winter (Edie 2001; Nagorsen 2006). The diet of ermine on Haida Gwaii is limited to the two native species of small mammal, as well as small birds, all of which are also prey for the larger, more abundant marten (Reid et al. 2000). Efforts to recover and maintain populations of secondary and primary consumers that are native to Haida Gwaii, including Haida ermine, should focus on riparian forests close to marine shorelines where competition for foraging habitat and risk of predation from marten is likely greatest (Hobson et al. 2000; Reid et al. 2000).

Chapter 4: Research Summary

Research findings

Marten (*Martes* spp.) function as apex predators on Haida Gwaii, British Columbia (BC), where the native mammalian community is devoid of most large and midsized carnivores that are found in adjacent mainland forests (Golumbia 2000). Industrial logging and introduced Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) have altered the age structure and distribution of canopy and understory plant species, with largely unknown long-term consequences for endemic species that are adapted to old-forest conditions (Gaston et al. 2002). As generalist predators with omnivorous diets, Pacific marten (*Martes caurina*) may benefit from the recent influx of introduced prey, most notably deer, with implications for conservation of species at risk (Reid et al. 2000).

I used camera traps to relate patterns of detection of Pacific marten with habitat attributes in coastal and inland areas. I attempted to accurately predict the probability of detecting marten across a study area that varied in the magnitude of forest harvesting, road density, and access to marine resources. I used stable-isotope analysis to quantify the spatio-temporal variation in marten diet. I estimated relative contributions of salmon, marine invertebrates, terrestrial fauna (beetles, mammals, and birds), and berries, to marten diet across seasons and during overall lifetime. I was able to determine how diet varied with different levels of access to marine resources, including salmon and marine invertebrates.

Marten detections were positively correlated with the linear density of roads and forest edges, habitat associated with the distribution of Sitka black-tailed deer (Gaston et al. 2002; Côté et al. 2004). The stable isotope analysis suggested that terrestrial fauna, including deer, contributed more than other diet items to the lifetime diet of marten. High rates of detection at

roadside trap stations in this study, as well as good capture success of commercial trappers, could be due to increased marten activity along roadsides where deer carcasses are more likely to occur (Reid et al. 2000; Carlson et al. 2014).

Results from this study support the hypothesis that marten on Haida Gwaii regularly use intertidal zones as foraging habitat (Foster 1963; Giannico & Nagorsen 1989). Marten were more likely to be detected near marine shorelines and estimates from the stable-isotope analysis suggested that marine invertebrates were an important diet item during all seasons. Marine shorelines are a rich and reliable source of nutrients, capable of supporting higher densities of mesocarnivores than inland habitats (Rose & Polis 1998; Linnell et al. 2018; Eriksson et al. 2019). However, marine invertebrates were relatively important to lifetime diet regardless of distance to shoreline. Marten move great distances relative to their small body size (Moriarty et al. 2017). Marten that I sampled may have large annual ranges that could include intertidal and supralittoral zones as foraging habitat for short periods of the year, as is observed in other coastal populations of mesocarnivores (Rose & Polis 1998). Marine resources may support a high density of marten, regardless of the underlying spatial organization of the population.

I provide evidence that riparian areas and associated allochthonous resources are important for marten on Haida Gwaii. Marten detections decreased the farther trap stations were from riparian areas, and I estimated that salmon were an important diet item in summer and fall. The intake of marine-derived nutrients, including salmon, was greatest during the fall, coinciding with salmon spawning, and the isotope values for muscle decreased as the winter progressed. Previous research has found that marten with access to salmon-bearing streams shift their diet to consume more salmon when the abundance of small mammals is low (Ben-David et al. 1997). Marten may also transport allochthonous nutrients from riparian areas to inland forests through

the deposition of feces and salmon carcasses. Transportation of marine-derived nutrients can increase primary production in terrestrial ecosystems relative to forests with no marine subsidies (Ben-David et al. 1998; Crait & Ben-David 2007; Quinn et al. 2009).

Stable-isotope analysis of guard hair and muscle tissue suggested that berries were an important component of marten diet during summer and fall. Seasonal reliance on berries may benefit understory and canopy plants on Haida Gwaii (Gaston et al. 2002; Jordano et al. 2007). Marten disperse the seeds of understory plants, including *Vaccinium* and salal (*Gaultheria shallon*), hundreds of meters farther than birds (Hickey et al. 1999; Dorworth et al. 2001; Schaumann & Heinken 2002). The germination of *Vaccinium* seeds is enhanced by passage through the gastrointestinal tracts of marten, and defecation on downed logs and in old-growth forests favors seedling establishment (Schaumann & Heinken 2002). Seed dispersal and deposition by marten may be important for maintaining gene flow and plant regeneration among understory plants (Jordano et al. 2007).

This study contributes to our understanding of the variability in habitat and diet ecology among insular populations of Pacific marten in an understudied region of North America (Bissonette 1997; Manlick et al. 2019). Marten occur at low densities across most forests of northern North America, and are often associated with structurally complex, old forests (Delheimer et al. 2019). However, marten display extraordinary phenotypic and behavioral plasticity that reflect evolutionary adaptation to local climates, natural disturbance regimes, landscape heterogeneity, resource availability, predation risk, and interspecific competition (Baker 1992; Bissonette 1997; Manlick et al. 2019). Given sufficient structural complexity, overhead cover, and prey density, marten do not necessarily require old-growth forests of a particular species composition (Baker 1992; Poole et al. 2004; Eriksson et al. 2019). Marten on

Haida Gwaii showed no affinity for increased stand age, tree height, canopy cover, or near-ground cover. Instead, occurrence was correlated with the human disturbance of commercial logging and its associated creation of roads and forest edges, as well as proximity to marine shorelines, rivers, and streams. These habitats support, and in some cases are preferred by, the predominant diet items consumed by marten.

Management recommendations

From the perspective of species distribution and abundance, marten are the top carnivore on Haida Gwaii, and may contribute to the healthy functioning of ecosystems by regulating plant and animal communities, and performing important ecosystem services (Dorworth et al. 2001; Darimont et al. 2008; McNicol 2019). However, several species of conservation concern may be outcompeted by marten for shared resources in a landscape altered by logging and introduced species (Reid et al. 2000; Waterhouse et al. 2017; Parks Canada 2018). Conservation and management planning should consider the spatial distribution and foraging ecology of marten to increase the effectiveness of habitat protection in coastal areas, and to decrease the potential for conflict between marten and competing species at risk.

My findings suggest that old forests retained in unharvested patches of at least 0.03 km^2 (3 ha) will increase the probability of use by marten. Forest edges and roadsides may function as foraging habitat for marten when diet is composed mainly of edge species and when there is low risk of mortality from predation or trapping. Forest management activities on Haida Gwaii should approximate patterns of tree mortality that would be present given the natural disturbance regime, including long return intervals between stand-replacing events and gap dynamics due to individual tree death. These patterns may result in decreased edge habitat and interspersion of

seral stages, lowering the carrying capacity for introduced deer (Franklin et al. 1987; Côté et al. 2004; Lindenmayer et al. 2012a).

Within 10 km of marine shorelines, marten were more likely to be detected closer to shorelines, and within 1 km of riparian areas marten were more likely to be detected closer to streams. Results from the stable-isotope analysis suggest that marine invertebrates are the main allochthonous nutrient subsidy to lifetime diet, and that salmon are taken seasonally when they become available during fall runs. These findings are supported by previous research showing that marine shorelines function as foraging habitat for Pacific marten in coastal areas (Eriksson et al. 2019; Manlick et al. 2019). Forests within 10 km of marine shorelines should be protected from harvest and human development in order to support multiple species of native carnivore. Forests within 1 km of riparian areas should be considered high-quality habitat for marten, with the probability of use increasing with proximity to the stream. Preference for forests located close to water, as well as intertidal foraging behavior, have been recorded for other species of carnivore on Haida Gwaii (Hobson & Sealy 1991; Reid et al. 2000); riparian forests along marine shorelines may contain the highest diversity of carnivore species and should be considered critical areas for protection.

I did not study fine-scale habitat features such as denning and resting sites, decadent snags, or large-diameter live trees. Also, I did not attempt to quantify prey density at sampling locations (Baker 1992; Bull & Heater 2000; Delheimer et al. 2019). Future research should focus on estimating marten density, as well as fine-scale habitat selection by marten on Haida Gwaii, including resting and denning structures. Additionally, research should attempt to determine the role of introduced prey, including deer, in marten diet. DNA metabarcoding is a promising new tool capable of determining contents of marten scat at a high taxonomic resolution (Eriksson et

al. 2019). Such a study should be carried out in all seasons to determine if habitat and diet ecology depend on seasonal fluctuations in prey availability and reproductive requirements (Zielinski et al. 2015).

Ecosystem-based management and intergovernmental co-management with the Council of Haida Nation have resulted in conservation-focused land-use practices on Haida Gwaii (Haida Gwaii Management Council & Province of British Columbia 2007). The Haida Gwaii Land Use Objectives Order provides management guidelines for conservation of endemic and at-risk forest-dwelling species such as Haida ermine (*Mustela erminea haidarum*), Northern Saw-whet Owl (*Aegolius acadicus brooksi*), and Northern Goshawk (*Accipiter gentilis laingi*) (Ministry of Agriculture and Lands 2014; Todd et al. 2018). Resource competition and intraguild predation by marten may limit recovery of these species where their foraging habitats overlap (Reid et al. 2000; COSEWIC 2006; Parks Canada 2018). Knowledge of the ecology of Pacific marten, a species that functions as an apex predator in insular island ecosystems, has direct applications to the conservation and recovery of endemic species at risk, and should be integrated into whole ecosystem-based approaches for managing cultural, biological, and economic forest values.

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Appendix A – Summary of model parameters (Table A1) and selection statistics (Table A2) for all candidate models, as well as coefficients from top models (Table A3), of Pacific marten detections on southern Graham Island, Haida Gwaii, British Columbia, Canada, between January and April, during 2017 and 2018.

Table A1. Values of habitat variables included in candidate mixed-effects logistic regression models for Pacific marten detections at trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, during winters of 2017 and 2018.

			All Stations (n = 72)				Marten not detected (n = 14)		Marten detected (n = 58)	
Category	**Variable (scale)**	**Units**	**Min**	**Max**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Forest structure	Average tree height* (100-m)	m	2.85	22.04	14.40	3.69	12.99	3.79	14.84	3.54
	Area >20 m height* (1000-m)	%	15.15	58.67	45.54	9.30	47.17	8.11	45.13	9.68
	Area 10–20 m height* (1000-m)	%	0.00	46.05	23.47	11.70	27.09	10.11	23.10	12.22
	Canopy cover* (100-m)	%	34.59	100.00	83.90	15.75	81.15	19.55	84.87	15.11
	Area >45% canopy cover (1000-m)	%	34.83	100.00	79.85	16.25	83.75	12.86	79.45	17.13
	Percent cover 0-1 m height* (1000-m)	%	92.98	100.00	96.68	2.02	96.45	2.37	96.70	2.01
	Percent cover 0-1 m height* (100-m)	%	90.78	100.00	96.95	2.18	97.15	2.40	96.84	2.16
	Average age (100-m)	years	36.64	408.00	166.59	117.93	152.11	133.21	165.02	115.32
	Area >250 years old (1000-m)	%	0.00	64.01	22.74	17.28	21.85	20.48	22.81	17.05
Topography	Distance to marine shoreline (100-m)	km	0.04	14.99	6.40	4.69	5.88	4.74	6.16	4.85
	Distance to riparian area (100-m)	km	0.04	2.29	0.48	0.38	0.48	0.31	0.49	0.42
Human disturbance	Area cut (1000-m)	%	0.00	56.66	8.63	12.03	5.43	9.19	9.75	12.94
	Area cut (100-m)	%	0.00	100.00	6.56	19.08	10.19	25.94	6.19	18.63
	Forest edge density (1000-m)	km/km^2	0.00	6.30	1.57	1.53	1.74	1.51	1.54	1.57
	Forest edge density (100-m)	km/km^2	0.00	7.27	1.56	1.71	1.75	1.75	1.55	1.74
	Road density (1000-m)	km/km^2	0.16	3.72	1.66	0.84	1.91	0.93	1.58	0.83
	Road density (100-m)	km/km^2	0.00	3.95	1.67	0.95	1.98	1.05	1.58	0.93
	Active road density (100-m)	km/km^2	0.00	2.21	0.84	0.50	1.03	0.43	0.79	0.52
	Abandoned road density (1000-m)	km/km^2	0.00	2.22	0.85	0.72	0.97	0.85	0.81	0.71
	Abandoned road density (100-m)	km/km^2	0.00	2.82	0.85	0.83	0.99	0.95	0.80	0.82

* indicates predicted LiDAR metrics.

Table A2. Candidate mixed-effects logistic regression models with model selection statistics for Pacific marten detections at trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, during winters of 2017 and 2018. Fixed effects are defined in Table 1.

Rank	Logistic regression models (scale)	k	LL	AIC_c	ΔAIC_c	AIC_c w_i
1	Area cut + Forest edge density ^{q} + Road density ^{q} + Station clustering + Year of sampling + Average temperature (100-m)	10	-298.88	617.81	0.000	0.208
2	Station clustering + Year of sampling + Average temperature (aspatial)	5	-304.17	618.35	0.537	0.159
3	Distance to marine shoreline ^{q} + Station clustering + Year of sampling + Average temperature (100-m)	7	-302.69	619.40	1.588	0.094
4	Distance to riparian area ^{q} + Station clustering + Year of sampling + Average temperature (100-m)	7	-302.82	619.66	1.850	0.083
5	Percent cover 0–1 m height* + Station clustering + Year of sampling + Average temperature (1000-m)	6	-303.91	619.84	2.029	0.076
6	Station density + Station clustering + Year of sampling + Average temperature (1000-m)	6	-304.02	620.06	2.251	0.068
7	Area >45% canopy cover + Station clustering + Year of sampling + Average temperature (1000-m)	6	-304.14	620.30	2.489	0.060
8	Average age + Station clustering + Year of sampling + Average temperature (100-m)	6	-304.17	620.35	2.541	0.058
9	Abandoned road density ^{q} + Active road density + Station clustering + Year of sampling + Average temperature (100-m)	8	-302.38	620.79	2.975	0.047
10	Area >20 m height*+ Area 10–20 m height* + Station clustering + Year of sampling + Average temperature (1000-m)	7	-303.76	621.55	3.737	0.032
11	Canopy cover*+ Average tree height* + Percent cover 0–1 m height* + Station clustering + Year of sampling + Average temperature (100-m)	8	-302.77	621.58	3.773	0.032
12	Null model (intercept with no covariates)	2	-308.91	621.82	4.007	0.028
13	Road density ^{q} + Area cut ^{q} + Station clustering + Year of sampling + Average temperature (1000-m)	9	-302.04	622.12	4.307	0.024
14	Active road density + Abandoned road density ^{q} + Forest edge density ^{q} + Station clustering + Year of sampling + Average temperature (1000-m)	10	-301.15	622.35	4.535	0.022
15	Area >45% canopy cover + Area 10–20 m height* + Area >250 years old + Station clustering + Year of sampling + Average temperature (1000-m)	8	-303.94	623.91	6.096	0.010

* indicates predicted LiDAR metrics

^{q} indicates two-term quadratic functions.

Table A3. Coefficients and statistical parameters for the most well-supported logistic regression models describing Pacific marten detections at trap stations on southern Graham Island, Haida Gwaii, British Columbia, Canada, during winters of 2017 and 2018.

						95% CI	
Conceptual Model	**Variables**	**Coefficient**	**SE**	**z**	**P > z**	**Lower**	**Upper**
Area harvested, forest edge, and road density	Cut	-0.023	0.011	-2.05	0.041	-0.046	-0.001
	Edge	0.131	0.258	0.51	0.612	-0.375	0.637
	edge2	-0.010	0.048	-0.21	0.833	-0.104	0.084
	Roads	0.641	0.601	1.07	0.287	-0.538	1.819
	roads2	-0.244	0.162	-1.51	0.131	-0.561	0.073
	Cluster	-0.133	0.406	-0.33	0.743	-0.928	0.662
	Year	0.690	0.422	1.64	0.102	-0.137	1.518
	Temp	-0.134	0.055	-2.42	0.016	-0.243	-0.025
Sampling bias	Cluster	0.028	0.417	0.07	0.946	-0.789	0.845
	Year	0.942	0.443	2.13	0.033	0.075	1.810
	Temp	-0.134	0.055	-2.42	0.015	-0.243	-0.026
Distance to marine shoreline	Marine	-0.265	0.161	-1.65	0.099	-0.579	0.050
	marine2	0.018	0.012	1.49	0.135	-0.006	0.042
	Cluster	-0.025	0.409	-0.06	0.952	-0.826	0.777
	Year	0.480	0.507	0.95	0.344	-0.513	1.472
	Temp	-0.132	0.055	-2.39	0.017	-0.240	-0.024
Distance to riparian area	Rip	-1.299	1.010	-1.29	0.198	-3.278	0.680
	rip2	0.911	0.579	1.57	0.116	-0.225	2.046
	Cluster	0.178	0.421	0.42	0.672	-0.647	1.003
	Year	1.003	0.442	2.27	0.023	0.136	1.871
	Temp	-0.133	0.055	-2.42	0.016	-0.242	-0.025

Appendix B – Mean isotope values of diet groups for Pacific marten by season (Table B1), as well as corrections applied to raw isotope values of diet groups (Table B2) collected on Haida Gwaii, British Columbia, Canada, between 2005–2018.

Table B1. Uncorrected isotope values used in Bayesian isotopic mixing models to estimate relative proportions of diet items in Pacific marten diet, collected on Haida Gwaii, British Columbia, Canada, between 2005–2018.

	Group (*n*)	**Mean δ13C**	**SD**	**Mean δ15N**	**SD**
Diet Items					
	Salmon (40)	-20.45	1.19	11.92	1.58
	Marine invertebrate (93)	-17.65	2.74	8.75	2.17
	Terrestrial fauna (223)	-26.28	0.48	4.14	0.61
	Berry (66)	-32.54	4.63	-1.19	3.11
Marten Tissue type	Distal guardhair (121)	-22.32	1.38	8.97	2.01
	Proximal guardhair (121)	-21.89	1.33	8.89	1.73
	Muscle (104)	-24.17	1.75	9.10	1.51
	Bone (122)	-21.29	0.99	7.73	1.16
Salmon density (proximal guardhair)	≤0.22 km/km2 (35)	-22.02	1.34	8.25	1.88
	0.22 - 0.60 km/km2 (53)	-21.90	1.39	9.29	1.62
	≥0.60 km/km2 (33)	-21.75	1.25	8.92	1.55
Distance to marine shoreline (bone)	≤2.6 km (26)	-21.30	1.01	7.73	1.10
	2.6 - 10.7 km (67)	-21.24	0.88	7.88	1.07
	≥10.7 km (29)	-21.38	1.22	7.36	1.36
Age class (proximal guardhair)	Juvenile (52)	-21.46	1.33	9.22	1.59
	Adult (57)	-22.38	1.17	8.57	1.67
Sex (proximal guardhair)	Female (47)	-21.18	1.32	9.07	1.95
	Male (73)	-22.35	1.13	8.77	1.58
Nutritional condition (bone)	Poor, Fair, & Good (69)	-21.29	1.07	7.91	1.19
	Excellent & Obese (52)	-21.29	0.89	7.47	1.10

Table B2. Mean isotope values of diet items by diet group used in Bayesian isotopic mixing models to estimate relative proportions of diet items in Pacific marten diet, collected on Haida Gwaii, British Columbia, Canada, between 2005–2018.

			δ13C		δ15N	
Diet Group	**Diet Item**	***n***	**Mean**	**SD**	**Mean**	**SD**
Salmon	Chinook salmon (*Oncorhynchus tshawytscha*)	6	-19.96	1.63	13.97	0.80
	Chum salmon (*Oncorhynchus keta*)	27	-20.82	0.79	11.06	0.91
	Coho salmon (*Oncorhynchus kisutch*)	7	-19.44	1.48	13.45	1.34
Marine invertebrate	Amphipod (Amphipoda)	23	-19.46	2.33	8.71	1.78
	Crab spp. (Malacostraca)	47	-16.30	2.16	7.99	2.19
	Marine snail (Gastropoda)	14	-17.99	3.13	10.32	1.92
	Blue mussel (Bivalvia)	9	-19.55	2.03	10.38	1.17
Terrestrial fauna	Sooty Grouse (*Dendragapus fuliginosus*)	6	-27.54	1.03	-1.30	1.43
	Red Crossbill (*Loxia curvirostra*)	1	-25.42	-	4.93	-
	Fox Sparrow (*Passerella iliaca*)	2	-25.00	1.63	4.66	1.22
	Song Sparrow (*Melospiza melodia*)	7	-24.63	1.24	4.75	1.96
	Swainson's Thrush (*Catharus ustulatus*)	1	-25.41	-	5.91	-
	Hermit Thrush (*Catharus guttatus*)	3	-25.89	0.58	5.23	0.50
	Varied Thrush (*Ixoreus naevius*)	3	-24.29	1.37	4.21	3.03
	American Robin (*Turdus migratorius*)	1	-24.60	-	6.81	-
	Brown Creeper (*Certhia americana*)	1	-25.44	-	8.10	-
	Orange-crowned Warbler (*Vermivora celata*)	1	-27.42	-	2.95	-
	Townsend's Warbler (*Setophaga townsendi*)	4	-26.42	1.15	4.23	1.81
	Warbler spp.	1	-27.95	-	3.17	-
	Golden-crowned Kinglet (*Regulus satrapa*)	3	-27.81	0.41	3.98	0.63
	Pacific Wren (*Troglodytes pacificus*)	5	-26.42	0.42	5.08	1.76
	Red-breasted Sapsucker (*Sphyrapicus ruber*)	1	-25.70	-	3.06	-
	Hairy Woodpecker (*Picoides villosus picoides*)	1	-19.17	-	12.00	-
	Northern Flicker (*Colaptes auratus*)	3	-27.16	1.81	6.13	0.50
	Red squirrel (*Taimasciurus hudsonicus lanuginosus*)	17	-22.10	1.18	3.68	2.23
	Sitka black-tailed deer (*Odocoileus hemionus sitkensis*)	16	-27.67	0.67	3.29	1.66
	Muskrat (*Ondatra zibethicus osoyoosensis*)	2	-27.82	1.99	5.40	1.77
	Keen's mouse (*Peromyscus keeni*)	49	-25.87	2.27	4.06	2.30
	Norway rat (*Rattus norvegicus*)	29	-22.07	3.00	8.44	2.21
	Black rat (*Rattus rattus*)	18	-25.23	0.60	6.29	1.39
	Rat (*Rattus* spp.)	3	-25.05	0.34	7.20	1.10
	Dusky shrew (*Sorex monticolus*)	14	-25.61	1.33	5.31	1.13
	Terrestrial beetle (Carabidae)	31	-28.11	1.44	4.04	1.60
Berry	Oval leaf blueberry (*Vaccinium ovalifolium*)	5	-39.83	3.22	-0.63	1.06
	Red huckleberry (*Vaccinium parviflorum*)	25	-35.29	4.10	-0.75	3.02
	Salal (*Gaultheria shallon*)	36	-29.62	2.29	-1.69	3.41

Table B3. Mean isotope values of diet items (with sample size) by sampling season, collected on Haida Gwaii, British Columbia, Canada, between 2005–2018.

Diet Item (*n*)	Season	Mean δ13C	SE	Mean δ15N	SE
berries (33)	Fall	-34.34	0.97	-0.23	0.57
berries (5)	Spring	-30.36	0.15	-0.87	1.19
berries (10)	Summer	-33.88	0.20	-1.86	0.34
berries (18)	Winter	-29.10	0.32	-2.37	0.82
marine invertebrates (39)	Fall	-17.82	0.46	9.10	0.32
marine invertebrates (9)	Spring	-17.68	1.17	6.85	1.06
marine invertebrates (45)	Winter	-17.49	0.37	8.83	0.29
salmon (32)	Fall	-20.48	0.19	11.55	0.25
salmon (3)	Summer	-20.44	1.30	13.48	0.34
salmon (5)	Winter	-20.24	0.61	13.35	0.73
terrestrial fauna (107)	Fall	-24.94	0.30	4.98	0.30
terrestrial fauna (44)	Spring	-25.64	0.37	5.21	0.41
terrestrial fauna (41)	Summer	-26.10	0.27	4.44	0.25
terrestrial fauna (29)	Winter	-26.28	0.39	4.52	0.39

Table B4. Corrections applied to raw isotope values to account for variable elemental concentration and trophic enrichment among diet items for Pacific marten collected on Haida Gwaii, British Columbia, Canada, between 2005–2018.

Diet Item (*n*)	Mean % C (SD)	Mean % N (SD)	δ^{13}C TEF (SD)	δ^{15}N TEF (SD)
berries (66)	34.66 (9.36)	0.83 (0.50)	2 (0.68)	3 (1.02)
m.invert (93)	31.14 (8.26)	5.60 (2.53)	1 (0.34)	3 (1.02)
salmon (40)	41.83 (10.13)	13.29 (3.33)	1 (0.34)	2 (0.68)
t.fauna (223)	45.35 (4.43)	12.77 (1.77)	2 (0.68)	3 (1.02)